Universidade de Aveiro Departamento de Biologia
Ano 2017

Pedro Correia Rodrigues

Influência das variáveis oceanográficas na distribuição de aves marinhas

Influence of oceanographic variables on seabird distributions

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia, realizada sob a orientação científica do Prof. Doutor Carlos Manuel Martins Santos Fonseca, Professor Associado com Agregação do Departamento de Biologia da Universidade de Aveiro.

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Dedico este trabalho aos meus filhos, à minha esposa, à minha querida Mãe e à memória do meu Pai.

I dedicate this work to my sons, to my wife, to my dear mother and to the loving memory of my father.

o júri

presidente

Prof. Doutor António Manuel Rosa Pereira Caetano
professor catedrático da Universidade de Aveiro

Prof. Doutor Carlos Manuel Martins Santos Fonseca
professor associado com agregação da Universidade de Aveiro

Prof. Doutor José Vítor de Sousa Vingada
professor auxiliar da Universidade do Minho

Doutor Vítor Hugo Rodrigues Paiva
investigador de Pós-Doutoramento do MARE - Centro de Ciências do Mar e do Ambiente, Universidade de Coimbra

Doutor João Paulo Campbell Alves da Silva
investigador de Pós-Doutoramento do CIBIO - Centro de Investigação em Biodiversidade e Recursos Genéticos / InBIO - Rede de Investigação em Biodiversidade e Biologia Evolutiva, Universidade do Porto

Doutor José Augusto Belchior Alves
investigador de Pós-Doutoramento do CESAM - Centro de Estudos do Ambiente e do Mar, Universidade de Aveiro

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palavras-chave

Aves marinhas, variáveis oceanográficas, ecologia espacial, modelos preditivos, planeamento espacial.

resumo

O desenvolvimento de estratégias efetivas de conservação para aves marinhas depende largamente do grau de conhecimento acerca da distribuição das espécies e a sua relação com o meio marinho.

Compreender as respostas das espécies às mudanças ambientais, em particular as variações no seu domínio vital e distribuição, é atualmente um dos maiores desafios para ecologistas e conservacionistas. A capacidade das espécies para alterarem a distribuição dependerá dos constrangimentos impostos pela qualidade e disponibilidade de habitat. As consequências para o aumento populacional e conservação dependerão dos benefícios associados com a ocupação de novos locais. O desenvolvimento de modelos robustos requer a quantificação adequada das variações de fatores ambientais, bem como a capacidade de seguir, remotamente ou in situ, os indivíduos no espaço e tempo.

O objetivo dos Modelos de Distribuição de Espécies, em particular o mapeamento preditivo, é providenciar informação espacialmente explícita acerca da ocorrência das espécies e de outros elementos ecológicos relevantes para o planeamento espacial de acções de conservação. O Planeamento Espacial para Conservação é uma abordagem multidisciplinar que permite identificar áreas importantes para a biodiversidade e atingir de forma eficiente objetivos conservacionistas específicos.

Os principais objetivos deste trabalho são (1) compreender os principais fatores ambientais que afetam a distribuição das espécies alvo, (2) compreender os domínios vitais e estratégias de alimentação, em relação às colónias, de cada espécie ou grupos alvo de estudo, (3) produzir modelos preditivos de distribuição de cada espécie ou grupos alvo de estudo e (4) desenvolver e implementar abordagens, baseadas em ferramentas estatísticas e de planeamento espacial, para identificar áreas ecologicamente relevantes para a conservação das espécies alvo.

keywords

Seabirds, oceanographic variables, spatial ecology, predictive models, spatial planning.

abstract

The development of effective conservation strategies for seabirds depends largely on the knowledge of species distributions and their relationship with the marine environment.

Understanding species responses to environmental changes, and particularly shifts in their range size and distribution, is therefore a major current challenge for ecologists and conservationists. The capacity of species to shift distribution will depend upon the constraints imposed by habitat quality and availability, and the consequences for population growth and conservation will depend on the fitness benefits associated with the occupation of new sites. Model systems require well-quantified range changes and the capacity to track individuals in space and time.

The purpose of Species Distribution Models, in particular predictive mapping, is to provide spatially explicit information on species occurrence and other ecological factors relevant for conservation planning. Spatial Conservation Planning is a multidisciplinary approach that allows to identify important areas for biodiversity and efficiently achieve conservation goals.

Our main objectives in this study are (1) to understand the main environmental determinants affecting the distribution of the target species, (2) to evaluate home ranges and feeding strategies, in relation to breeding colonies, of different species or target groups, (3) to produce accurate seasonal probability distribution models for each species or target groups (4) to establish procedures based on statistic and spatial tools to identify ecologically relevant areas for species conservation.

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General Introduction

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General Introduction

Introduction

The study of animal movement and use of space combined with predictive distribution models are a powerful tool for understanding species ecology through their life cycles (habitat use and selection, habitat connectivity, recruitment, migration, and foraging strategies) and to investigate the impacts of human activities on biological processes (Tremblay et al. 2009b; Franklin 2010). This information is essential to develop appropriate conservation strategies for target species, particularly for those that occupy pelagic areas and undertake inter-continental movements, which are challenging to study regarding their life offshore as is the case of many seabirds.

In the marine environment, the processes that regulate the patterns of species distributions are still an area of intensive research (Tremblay et al. 2009a, 2009b). However, it is known that the spatial distribution of seabirds is influenced by several biophysical factors (Fauchald 2009; Wakefield et al. 2009) such as the topography and physiography of the ocean floor, sea surface temperature, salinity, concentrations of chlorophyll, currents, prey productivity and also by human-induced factors, such as pollution, noise or fishing activity (González-Solís & Shaffer 2009; Croxall et al. 2012). Understanding species distribution and the effect environmental factors play in promoting or constraining the use of specific areas is paramount for undertaking evidence based management and biodiversity conservation decisions (Sutherland et al. 2004; Pullin & Knight 2009). For instances, quantifying the spatial and temporal overlap between foraging seabirds and fishing and fishing method, is essential to reduce both the competition for same resources and the direct mortality of pelagic birds due to some types of fishing gear (Belda & Sánchez 2001; Tuck et al. 2011; Croxall et al. 2012).

Classical methods of acquiring information on animal occurrence in the marine environment, would mostly rely on hydrographic boat surveys, boat bird censuses or bird ringing at breeding colonies, and dead recoveries on the coast which generated very limited spatial-temporal information and would be severely biased. This was primarily due to the fact that the spatial mathematical processing of data was very limited until quite recently. However, both technological and computational techniques have evolved significantly over the past decade and at present, a number of suitable tools to collect detailed information on animal movement are available as well as to analyse positional data in a refined and detailed form (Croxall et al. 2005, 2012; Wilson et al. 2007; Aarts et al. 2008; Burger 2008; Bograd et al. 2010; Soanes et al. 2016). At the same time monitoring the marine environment via satellite is particularly useful for studying the environmental variables of habitats for species that exhibit great mobility, namely when it involves movements in pelagic waters of different economic zones or when migration movements are inter-continental (Ristow et al. 2000). From spatial optical observations of sea surface it is now possible to amass information from remote areas at a relatively reasonable cost, for a wide range of environmental characteristics, both physical (temperature of sea surface salinity, wind) and biological (ocean productivity, human disturbances, fishing effort distribution) (Rodhouse et al. 2001; Wilson et al. 2002). For example, biological productivity can be estimated from the phytoplankton abundance, which is estimated from the light absorbed by photosynthetic pigments, which in turn are calculated through optical biophysical data collected by satellite sensors. This information allows characterizing the different types of marine habitats and to investigate the interactions between them and bird distribution.

Current technological and industrial capacity of building various miniaturized instruments in order to be transported by medium sized seabirds, revolutionize the study of species which traditionally were impossible to track, most noticeable in pelagic habitats (Hunt & Wilson 2012). Among these animal tracking equipment, it stands out for their interest, relatively affordable prices and reduced dimensions the Light Level Geolocators (GLS)

loggers and the Global Positioning System (GPS) loggers. The weights of GLS loggers range from 0.3g upwards, while GPS loggers range from 2-3g upwards (depending on the models, battery capacity and spatial resolution). Current guidelines for instrumenting birds state that external devices should not exceed 3–5% of the birds' body mass (Kenward 2001; Vandenabeele et al. 2012).

The wide availability of remote sensing data, GPS devices and computing power led simultaneous developments on computer and statistical sciences, which now provide the methodological and theoretical frameworks for predictive ecology (Roberts et al. 2010). Nowadays, Geographic Information System (GIS) software allows the analytic integration of animal movement data and marine environmental variables, contributing to a better understanding of the multidimensional nature of marine ecosystems. Furthermore, the simplification of data sorting and preparation for species distribution modelling (e.g. spatially rarefying occurrence localities, preparation of climate data, and creation of background bias files) and the easy access to several statistical software packages, allowed the development of Species Distribution Models (SDMs) analysis (Guisan & Thuiller 2005) in predictive ecological studies (Brown 2014). In recent years, the mathematical algorithms and methodologies to analyse movement patterns and spatial modelling have evolved significantly (Aebischer et al. 1993; Guisan & Zimmermann 2000; Jonsen et al. 2003; Aarts et al. 2008; Wakefield et al. 2009) and multiple methods are currently available. A major distinction among these is the kind of species occurrence data they require (Elith et al. 2010). Analysis of species occurrence data collected systematically (presence-absence data) usually use regression methods, like generalized linear or additive models, GLMs or GAMs, or ensembles of regression trees, random forests or boosted regression trees, BRT (Elith & Graham 2009; Elith et al. 2010). However, most studies on species distributions are not based on systematic surveys due to the limited spatial coverage or other methodological or logistic constraints thus resulting in presence-only data. This is the case of most of studies involving seabird tracking. In general, most seabird species usually present a highly mobile behaviour (daily and/or seasonally), presenting relatively large

home ranges, which makes them particularly difficult to study at sea using standardized methods that require a good spatial coverage. Studies involving standardized census methodologies at sea usually are very expensive and involve complex logistics, therefore a suitable alternative is to track individual seabirds using bio-logging devices but attaining presence-only data. The necessity to maximize the utility of this kind of species occurrence data has led to the emergence of several SDM methods for modelling presence-only data. MaxEnt software package (Phillips et al. 2006) is particularly popular in species distribution/environmental niche modelling, most likely due to: (1) is one of the most practical methods for modelling species distributions; (2) it typically outperforms other algorithms based on predictive accuracy; (3) it requires only presence data plus environmental information for the entire study area. Phillips et al. (2006) and Elith et al. (2010) provide information about MaxEnt mathematical computations, while Merow et al. (2013) provides a detailed explanation of its mechanics.

Post-modelling analyses of species distribution models have also been simplified over time (e.g. assessment of the distributional changes between time periods or differences in habitat use between species, populations or sex) (Warren et al. 2010; Brown 2014). This simplification of processes usually relies on the development of software packages to automatize data processing, simplify outputs generation or facilitate decision making. One good example of this kind of software is Zonation, a publically available decision support system for spatial conservation planning. It produces a hierarchical prioritization of the landscape and identifies areas important for retaining habitat quality and connectivity for multiple species, indirectly aiming at species' long-term persistence. Zonation produces a complementarity-based priority ranking (Moilanen 2005). By combining SDM with spatial prioritization analysis it is possible to take biodiversity conservation actions, for instances by defining Marine Protected Areas (MPAs) (Kelleher 1999; Lascelles et al. 2016; Soanes et al. 2016).

Thesis objectives

This study aims to assess how relevant eco-geographical variables influence the distribution, at different spatio-temporal scales, of umbrella species for marine conservation. Using predictive distribution models, based on habitat suitability of the study areas, it aims to produce relevant tools to support decision-making and establish effective conservation and management plans. This is achieved by undertaking the following overall objectives:

1. Understand the distribution of target marine bird species in the study areas.

2. Evaluate home ranges and feeding strategies, in relation to breeding colonies, of different species or target groups.

3. Relate the occurrence of birds with relevant environmental and ecological variables (*eg*. bathymetry, slope, distance to shore, distance to colony, winds, productivity, sea surface temperature, salinity).

4. Identify, using modelling techniques, important areas for the conservation of species.

Thesis structure

This thesis is organized in five chapters. The first chapter presents a general introduction about the theme and aims of the thesis. Research questions are presented in the three following chapters (Chapter 2 to 4) in the format of scientific articles, specifically written for the thesis and adapted to manuscript format for future submission for publication. These papers are intended to be independent and mutually exclusive, thus some repetition may occur. The main findings of the research are summarized and generally discussed in the final chapter.

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Chapter 2

Tracing the steps of giants: modelling global distribution of sibling Giant Petrel species

Chapter 2

Tracing the steps of giants: modelling global distribution of sibling Giant Petrel species

Abstract

Northern and Southern Giant Petrels (*Macronectes halli* and *Macronectes giganteus*) are amongst the most pelagic bird species. We tracked 14 male and 11 female Northern Giant Petrels (NGP) and 13 male and 15 female Southern Giant Petrels (SGP), at Bird Island, South Georgia, using Geolocators. Seasonal species distribution models, for each species and sex group, were computed using MaxEnt. Giant Petrels' summer distribution seems to be strongly constrained by the proximity to breeding colony. It stands out that SGP have wider high-probability of occurrence areas around colonies and a greater niche breadth than NGP. Summer ecological niches clearly reflect the fact that both species are central place foragers. The winter models present clear evidences of post-reproductive dispersal effects, reflecting a latitudinal segregation between species. The two species seem to compete and share a common preference for the same environment. However, SGP seem to prefer intraspecific competition rather than to compete with NGP.

Introduction

The development of effective conservation strategies for seabirds depends largely on the knowledge of species distributions and their relationship with the marine environment. Early pelagic seabird tracking studies tended to describe habitat use qualitatively (Wakefield et al. 2009). But during recent years and as a response to the growing need for a thorough understanding of species geographical distribution, new predictive modelling techniques have been developed and improved, allowing to extrapolate potential distribution of species as a proxy for actual observations (Souza Muñoz et al. 2009; Franklin 2010). These approaches interpolate spatially occurrence data and eco-geographical variables (both biotic and abiotic factors) to create a model of species' environmental requirements, over large spatial scales (Anderson et al. 2003). Such computational advances led to the growth of an interdisciplinary approach, that uses Machine Learning methods to model complex ecological processes and patterns (Olden et al. 2008). One of these methods is MaxEnt, specifically designed to develop species distribution models (SDM) with "presence-only" occurrence data (Dudík et al. 2007). However, SDM applied to marine species requires the use of oceanic environmental predictors. But the ongoing technological revolution has allowed establishing a vast archive of remotely sensed data for the oceans and thus timely global oceanographic data from satellites are becoming readily available, for both pelagic and neritic environments. Many of these variables (e.g. sea water temperature), are mapped at a coarse spatial scale, which is unsurprising given the vast expanse and dynamic nature of the oceans, but this variation also limits the ability to establish valid correlations between marine species movements and habitat variables. (Franklin 2010). Nevertheless, these datasets allow attaining the environmental predictors in order to apply SDM to marine species.

Marine species pose a particularly difficult challenge with regard to their use of space as they perform vast movements during the different stages of their annual cycle. Remote-tracking studies during the last decade have greatly contributed to address this lack of information and have allowed new insights into the spatial component of trophic niches of seabirds (González-Solís et al. 2007; Burger and Shaffer 2008; Tremblay et al. 2009). Records obtained through remote-tracking can be considered as presence-only data, because they allow attaining information on species presence but don't allow inferring about absence, since this information is relative to a sample of the total population. Therefore, the number of tracked birds (sample size) will greatly influence the quality of the global information for the species distribution. In this sense, Light Level Geolocators (GLS) present two major advantages for these type studies. Firstly, their low energy consumption allows its use during long periods of time, which allows amassing movement data for a complete annual cycle. Secondly, these devices have a relatively low cost which allows, deployment on a larger sample of individuals at a low cost.

Northern and Southern Giant Petrels (*Macronectes halli* and *Macronectes giganteus*) are amongst the most pelagic bird species. These two sibling species have a sympatric distribution and coexist at a number of sub-Antarctic archipelagos (Hunter 1987, Patterson et al. 2008). Previous studies focused on their spatial ecology, comparing foraging areas exploited by individuals of the same colony and investigating interspecific and intersexual competition (González-Solís et al. 2000a, b; González-Solís et al. 2002; González-Solís et al. 2007).

Our main aims in this study were (1) to understand the ecological segregation and the main environmental determinants of the distribution of male and female northern and southern giant petrels, and (2) to produce accurate seasonal probability distribution models for each species and gender group, in order to obtain predictive occurrence maps at a global scale. These results can be used as a tool to implement conservation management actions.

Methods

Fieldwork

Fieldwork was carried out on Bird Island, South Georgia (54°, 03´S, 38° 36'W) in October to March 1999 to 2001. On this island, estimated breeding pairs of northern and southern giant petrels in 1996 was 2062 and 521, respectively (D.R.Briggs and R.Humpidge *in litt*.) (González-Solís et al. 2000a). The study colony comprised a few breeding aggregations of giant petrels from both species, sometimes breeding intermingled, totalling more than 150 nests for each species. In November 1999, we deployed 100 Geolocators (GLS) mounted on a Darvic ring in equal proportions on male and female northern and southern giant petrels during the incubation period. GLS were deployed on a single member of each pair to minimize any potential impact of the GLS on the breeding performance. We recovered 63, 7 and 1 GLS after 1, 2 and 3 years respectively, and downloaded complete data from 14 male and 11 female northern giant petrels and 13 male and 15 female southern giant petrels. Eleven GLS could not be recovered because they had fallen off the Darvic ring; the remaining 18 birds were not seen in the area over the following two years. The GLS used in this study were developed by the British Antarctic Survey and weighed 16 g. The GLS were equipped with an internal clock and measured the light levels every 60 s, recording the maximum reading within each 10 min interval (full details in (Afanasyev 2004). From this information 2 positions per day (one corresponding to midday and the other to midnight) can be inferred with an average accuracy of 186 km ± 114 km (Phillips et al. 2004a).

Positioning and filtering procedures

Positions were calculated using Multitrace-3/16 light (Jensen Software Systems, 1997) by inspecting the integrity of the light curve day by day and fitting dawn and dusk times. The elevation angle of the sun was set at -5.5. To filter unrealistic positions, we removed: (a) those obtained from light curves showing interferences at dawn or dusk (mainly due to the bird sitting on the ground or to the proximity of artificial light); (b) those inferred from days or nights longer than 23 hours; (c) those with a speed index (V_i) above 60 km/h, as calculated by the root of the square speed average of the segments formed with the two preceding and the two following positions (McConnell et al. 2004):

$$V_i = \sqrt{\frac{1}{4} \sum_{j=-2, j \neq 0}^{j=2} (v_{i,j+i})^2}$$

Where $V_{i,j+i}$ is the velocity between successive positions *i* and *j+i*; (d) those within the equinox periods ranging from 19 March to 9 April and from 3 to 29 September (we set the equinox periods after a graphical inspection of the behaviour of the speed index over the year). By this procedure we discarded 24.9% of 44,349 positions (González-Solís et al. 2007). The analyses of the relationships between positions and the environmental variables were restricted to an one year period, from 1st of November 1999 to the 31st October 2000 (25,847 positions).

Background information, data sources and geographical procedures

The main purpose of this work was to obtain predictive distribution maps at a wide geographical scale, so all data were converted to a WGS84 projection. Since we tracked the movements of giant petrels using GLS with a nominal accuracy of 186 km we analysed large-scale habitat selection. Thus, cell size was set to 2° x 2° and the study area was restricted to south of 25° South and north of 65° South, because: (1) this area reflects the potential

distribution range of both species; (2) the accuracy of the GLS further south is limited by the length of the day and night near the solstice periods; (3) most of the area below 65 º south is completely covered by ice (except in some areas in summer) and; (4) this area includes the minimum possible portions of land (which giant petrels could not visit apart from the coastal areas). To work on spatial data we used ESRI ArcGIS 9.2 and MiraMon (Pons 2000).

We considered a set of 16 eco-geographical variables (EGV) of three types: temporal environmental variables, static variables and spatial variables (Table 2). Static variables included bathymetry and bathymetry slope (derived from bathymetry). The temporal environmental variables tested for inclusion in the model were: chlorophyll a concentration, ice concentration, sea surface temperature, surface wind speed, surface wind direction and rain rate. Spatial variables included distance to giant petrel colonies, distance to seals colonies and distance to penguin colonies.

Bathymetry was obtained from the National Geographical Data Center from U.S.A. (ETOPO2; http://www.ngdc.noaa.gov/mgg/global/global.html). This also allowed us to calculate bathymetry slope, using GIS tools.

In addition, we obtained monthly data on the sea surface variables from November 1999 to November 2000 from the following sources: (1) Chlorophyll a concentration from the SeaWiFS project (http://daac.gsfc.nasa.gov/data/dataset/SEAWIFS/index.html); (2) Ice concentration from the British Atmospheric Data Center (BADC; http://badc.nerc.ac.uk/); (3) Sea surface temperature from the British Atmospheric Data Center (BADC; http://badc.nerc.ac.uk); (4) Surface wind speed from QuikScat (Remote Sensing Systems, www.remss.com); (5) Surface wind direction from QuikScat (Remote Sensing Systems, www.remss.com); (6) Rain rate from QuikScat (Remote Sensing Systems, www.remss.com). Based on these monthly data, we calculated seasonal averages for each of these dynamic variables. We didn't consider in this operation missing value raster cells, to avoid bias on average results.

Beside this subset of environmental dynamic variables, we decided to also include a group of spatial features we considered to have an ecological significance. Both Giant Petrels species are known scavengers and they depend on seals and penguin carcasses during breeding season. Therefore, it seemed important to include in the variable set EGV that could somehow reflect this ecological dependency on carrion availability. This was achieved by creating background layers that reflect distance to large seal colonies and distance to large penguin colonies in the study area, based on known colonies location and numbers. (González-Solís et al. 2007) extensively discussed offshore inter and intra specific spatial segregation in giant petrels. Thus, another predictive variable we considered to eventually have an ecological significance is distance to other giant petrel colonies.

We also considered important to evaluate the importance of distance to the several fronts: Polar Front, Subantarctic Front, Subtropical Front, Southern Antarctic Circumpolar Front and southern boundary of Antarctic Circumpolar Current. Information on location of these fronts was obtained from Orsi et al. (1995).

These background layers were calculated using the same computational procedure in ArcGIS 9.2 to calculate the least cumulative cost distance for each cell to the nearest source over a cost surface (excluding all portions of land from the cost surface raster).

Species Distribution Modelling Procedures

Classical habitat modelling techniques (e.g. Generalised Linear Model – GLM or Generalised Additive Model – GAM) are based on presence-absence data (Guisan and Zimmermann 2000, Redfern et al. 2006). The data collected using GLS only provides information about individuals' movement. Therefore, this kind of data doesn't allow one to make correct inferences about a species "true" absence. Thus we decide to use a presence-only method

to develop predictive distribution models for both sex groups of Northern and Southern Giant Petrel, during summer and winter sub-Antarctic seasons.

We have chosen software application MaxEnt 3.1.1, to compute these seasonal habitat suitability models, for each species and sex group, and obtain global predictive distribution maps based on probability of occurrence. Detailed description of MaxEnt and its mathematical computations are given in Phillips et al. (2006, 2004b).

MaxEnt is a general-purpose method for making predictions from incomplete information based on the maximum-entropy principle, which assumes that the best approximation to a unknown probability distribution is to ensure that it satisfies any constraints that we are aware of (Phillips et al. 2004b). Applied to presence only species distribution modelling, the idea is to estimate the distribution of a species as a probability distribution across a study region, subject to the constraints that each expected predictor variable has to match its empirical average over the presence sites. Of all the probability distributions that meet these constraints, MaxEnt choose the most unconstrained one, i.e. the one of maximum entropy (Phillips and Dudík 2008). Phillips et al. (2006) outlined several MaxEnt advantages: (1) It requires only presence data plus environmental information for the whole study area; (2) It can utilize both continuous and categorical data and can incorporate interactions between different variables; (3) MaxEnt algorithms have been developed in order to ensure the optimal probability distribution; (4) The results are amenable for interpretation of the form of the environmental response functions. This method has generated great interest because in comparisons it has shown higher predictive accuracy than many other methods when applied to "presence-only" species occurrence data (Elith et al. 2006, Franklin 2010).

Several studies compared MaxEnt to other presence-only methods with several placing MaxEnt on the top-performing methods in terms of prediction accuracy (Elith et al. 2006) or concluded that it performed somewhat better than other methods (Hernandez et al. 2006, Phillips et al. 2006, Pearson and Raxworthy 2007, Phillips 2008, Elith and Graham 2009).

We considered 4 independent sample sets (Table 1), based on species and sex: Northern Giant Petrels Males (NGPM), Northern Giant Petrels Females (NGPF), Southern Giant Petrels Males (SGPM) and Southern Giant Petrels Females (SGPF). So as to evaluate inter and intra-specific differences in habitat selection and distribution, we considered two different seasons for modelling procedures: Summer (November – March) and Winter (June-September). We deliberately excluded data relative to April, May and October because: (1) these are transition months between sub-Antarctic seasons; (2) to exclude from analysis less accurate positioning data collected around equinox periods.

Table 1 - Abbreviations for each model, accordingly with 3 group criteria: season, species and sex.

		Season	
		Winter	**Summer**
Northern Giant Petrel	**Male**	WNGPM	SNGPM
	Female	WNGPF	SNGPF
Southern Giant Petrel	**Male**	WSGPM	SSGPM
	Female	WSGPF	SSGPF

The objective was to build, for each species gender group, a seasonal model with adequate performance using the best subset of environmental variables. In brief, this would lead to the production of 8 predictive distribution maps, i.e. two seasonal maps for each species/sex group.

To accomplish this objective, the first step was to identify the EGV that are more important in predicting occurrence/habitat suitability. The Jackknife test of variable importance was

used to evaluate the relative importance of each predictor variable initially considered. The training gain is calculated for each variable alone, as well as the drop in training gain when the variable is omitted from the full model (Peterson et al. 2007). This way we computed an initial model using 16 eco-geographical variables and those with lowest decrease in average training gain when omitted were discarded (Table 2 – *List of eco-geographical variables considered as relevant to predict occurrence and habitat suitability.*). The results of this initial full model also revealed problems related with interactions between variables. We thus decided to reduce the number of variables, including only the most significant ones. To do so, we compared models including different sets of predictive variables and evaluated which had better performance. The area under the receiver operating characteristic curve statistic (AUC) was used to test each model's discriminative ability. We also analysed the Omission Rate and Fractional Predicted Area based on the 10 percentile value for presence (Table 3).

Table 2 – List of eco-geographical variables considered as relevant to predict occurrence and habitat suitability.

ID	Variable	Code	Discarded	Winter models	Summer models
1	Chlorophyll	*chla*	-	√	√
2	Ice	*ice*	-	√	√
3	Wind Direction	*wdir*	-	√	√
4	Wind Speed	*wspeed*	-	√	√
5	Rain Rate	*rain*	-	√	√
6	Sea Surface Temperature	*sst*	-	√	√
7	Bathimetry (DEM)	*DEM*	-	√	√
8	Slope	*slope*	-	√	√
9	Distance to Seals' Colonies	*dist_seals*	-	-	√
10	Distance to Penguins' Colonies	*dist_cpeng*	-	-	√
11	Distance to Giant Petrel Colonies	*dist_colgps*	-	√	√
12	Distance to Polar Front	*dist_pf*	-	√	-
13	Distance to Subantarctic Front	*dist_saf*	-	√	-
14	Distance to Subtropical Front	*dist_stf*	√	-	-
15	Distance to Southern Antarctic Circumpolar Current Front	*dist_saccf*	√	-	-
16	Distance to southern boundarie of Antarctic Circumpolar Current	*dist_sac*	√	-	-

Each model was projected to global study area, using as projection layer the variable distance to giant petrel colonies.

For each species/sex group, we randomly drew from each individual dataset an equal number of tracking locations. This way we equalized the weight of each individual in the sample, in order to guarantee that the models' results are representative of the study populations (Fieberg et al. 2010, Frair et al. 2010, Hebblewhite and Haydon 2010). We set

MaxEnt to remove duplicate presence records from the same grid cell to minimize autocorrelation biases. Model evaluation was realized with a two-fold cross validation, randomly selecting 70% of sample points as training data and 30% as test data.

Niche Overlap and Niche Breadth

In order to quantify the niche similarity between SDMs (amongst groups and between seasons), we used a niche overlap index. Warren et al. (2008) state there is no a priori justification for any particular measure of environmental-niche differentiation or similarity. We use a niche overlap index that compares our mean predicted probability distributions defined over geographic space, in which pX,i (or pY,i) denotes the probability assigned by the ecological niche model for species X (or Y) to cell *i* (Warren et al. 2008). The overlap metric employed comes from the ecological literature; Schoener's (1968) statistic for niche overlap (D),

$$\boldsymbol{D}\left(\boldsymbol{p}_{X,i}, \boldsymbol{p}_{Y,i}\right) = \mathbf{1} - \frac{\mathbf{1}}{\mathbf{2}} \sum_{i} \left|\boldsymbol{p}_{X,i} - \boldsymbol{p}_{Y,i}\right|,$$

ranges from 0 (niche models have no overlap) to 1 (niche models identical).

In addition, for each group, we calculated an estimate of niche breadth by applying a traditional measure of niche breadth (Levins 1968). Standardized breadth measurements range from 0 (one grid cell has a suitability of one, all other cells are zero), to 1, where all grid cells are equally suitable (Mandle et al. 2010, Nakazato et al. 2010).

These metrics do not require application of a threshold to produce predictions of presence and absence, but rather uses the continuous estimates of habitat suitability directly produced by MaxEnt. Niche overlap and niche breadth test were conducted using ENM Tools 1.3 (Warren et al. 2008, 2010).

Results

Though having a high AUC score, visual inspection of model results led us to decide to exclude some of the 16 initial variables, to correct artefacts resulting from interactions between correlated variables. These correlations were causing evident misleading predictions in some specific geographical areas. This way, after analysing the global model Jackknife results, AUC scores and considering the ecological meaning of each eco-geographical variable, we decided it was more coherent to consider different groups of eco-geographical variables accordingly to season. Both species are more dependent on carrion availability during breeding season and have a more pelagic foraging behaviour during non-breeding season. Summer and winter model variables are described in Table 2. We thought it would be important that final predictive maps could somehow reflect also the weight of colony size. To do so, we projected the models considering two different sets of information: a. using locations of all Giant Petrel colonies; b. using information on locations of large Giant Petrel colonies (more than 300 breeding pairs). We then overlapped the results of both projection scenarios and calculated mean results. This procedure allowed us to attribute less weight to isolated small colonies, without completely excluding their importance from the final predictions.

Model fitting procedures provided models with high AUC scores, for both training and test datasets (Table 3). The minimum values for training and test AUC were 0.923 and 0.966, respectively, meaning that all models have good predictive performances.

Table 3 – Training AUC, Test AUC and 10 percentile threshold scores for each seasonal model, calculated using different species/gender group datasets.

		AUC		10 PERCENTILE TRESHOLD		
		Training AUC	Test AUC	Training Omission Rate	Test Omission Rate	Fractional predicted area
Summer	NGPM	0.968	0.983	0.099	0.019	0.064
	NGPF	0.972	0.985	0.095	0.022	0.052
	SGPM	0.958	0.982	0.098	0.020	0.098
	SGPF	0.923	0.969	0.098	0.032	0.179
Winter	NGPM	0.962	0.966	0.096	0.052	0.075
	NGPF	0.971	0.978	0.099	0.016	0.054
	SGPM	0.964	0.987	0.099	0.007	0.077
	SGPF	0.929	0.969	0.100	0.018	0.175

Jackknife test results show that *dist_colgps* is the most useful variable to explain the distribution of each group, on both season, since it has the highest regularized training gain with only variable (Figure 1). MaxEnt Jackknife analysis also selected as important variables, to all groups and for summer models, *dist_seals*, *dist_cpeng* and *chla_sum*. Regarding winter models, jackknife results also identified *sst_win*, *wspeed_win* and *chla_win* as important variables to predict NGP male and female distributions; *sst_win*, *chla_win* and *wdir_win* are also important EGV to predict SGP male and female occurrence areas.

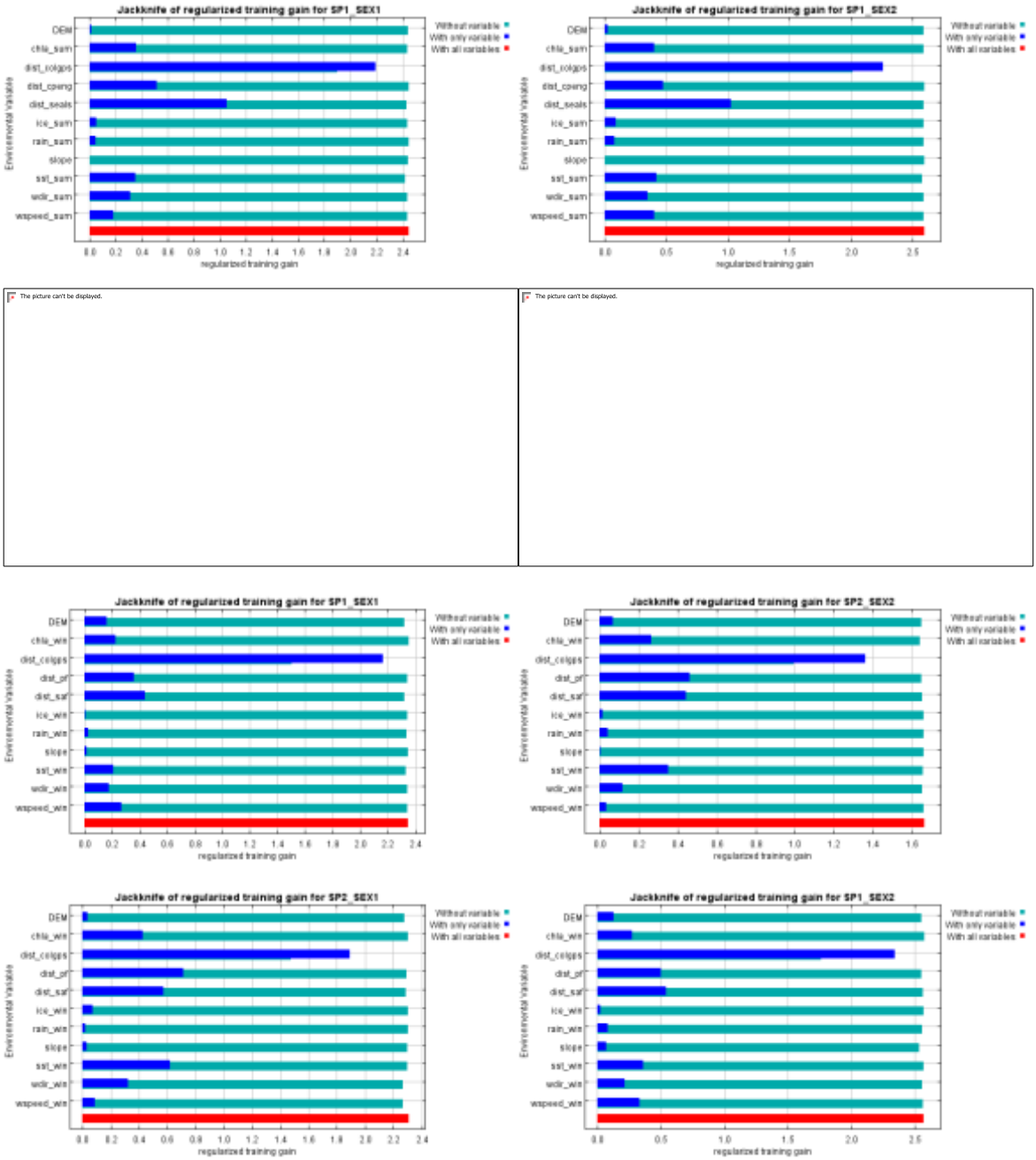

Figure 1 - Jackknife test results for each seasonal species/sex group model: Northern Giant Petrel Males (SP1_SEX1), Northern Giant Petrel Females (SP1_SEX2), Southern Giant Petrel Males (SP2_SEX1) and Southern Giant Petrel Females (SP2_SEX2).

The summer distribution models predicted high-suitability areas centred around Giant Petrel colonies, although they differ for each group in the predicted extent of that area (Figure). For instance, SGPF is the group with wider high-probability of occurrence areas during summer months. On the other hand, NGPF is the group with shorter range high-probability areas. Winter predictions are noticeably different for both species. Both SGP groups have wider high-probability areas than NGP groups, and cells with higher scores are located more to the South, with a more evenly longitudinal distribution. SGPM have a broader high-probability area than SGPF. For NGP males and females, the highest scores are located closer to land. NGPM winter model aggregates high-probability areas around large colonies, as well as around coastal areas (north coast of Argentina, Uruguay, South Africa and Tasman Sea). NGPF winter model shows a similar distribution pattern, but in general MaxEnt probability scores are lower than NGPM, meaning that it is harder to predict this group's winter distribution.

Predictive models outputs show that, for both seasons, NGP have more fragmented potential occurrence areas than SGP. SGPM and SGPF occurrence areas suggest a higher potential for population connectivity over a larger region (presence/absence binary maps available in Appendix supporting information).

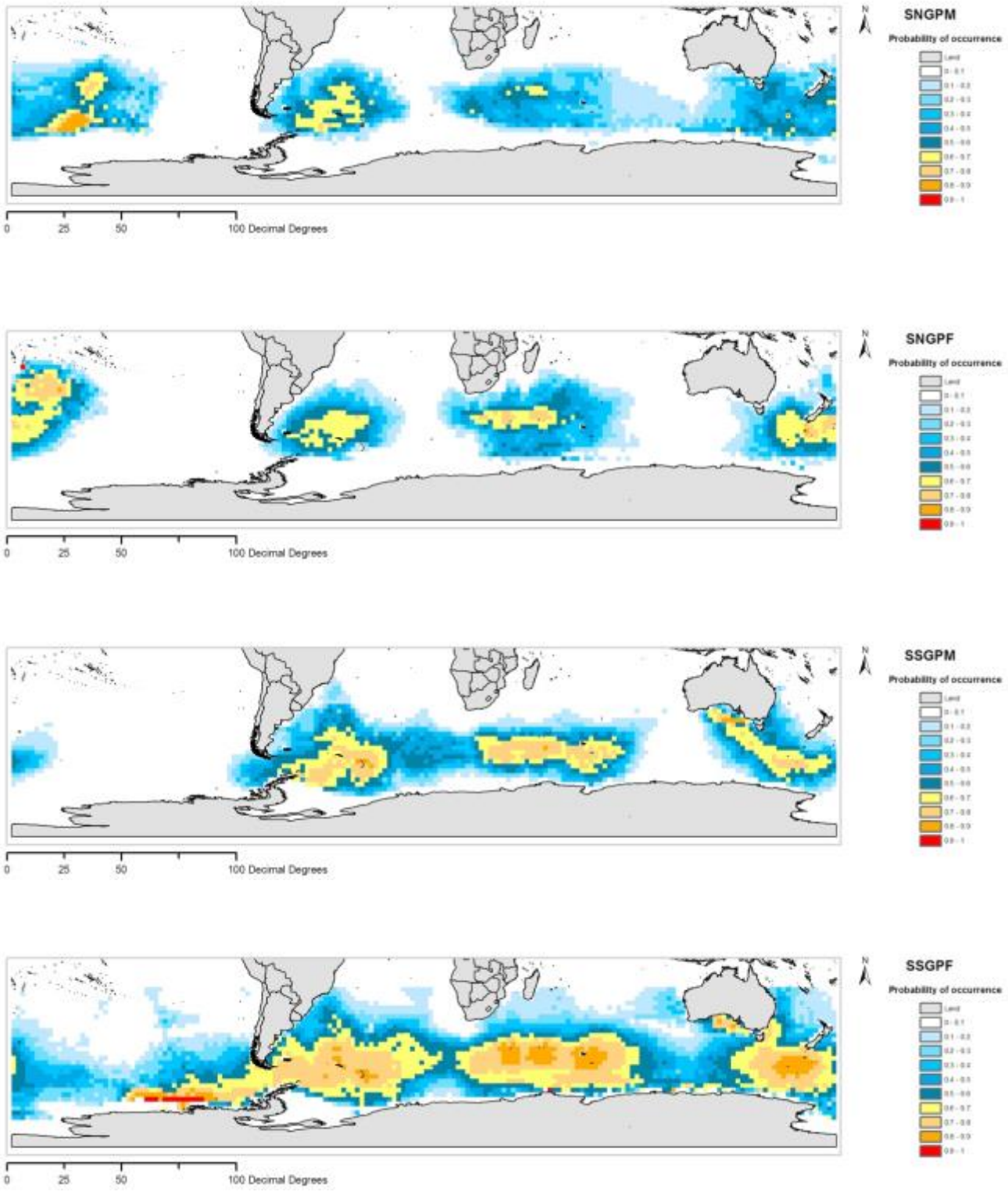

Figure 2 - Global predictive distribution maps based on the projection of each seasonal species/sex group model.

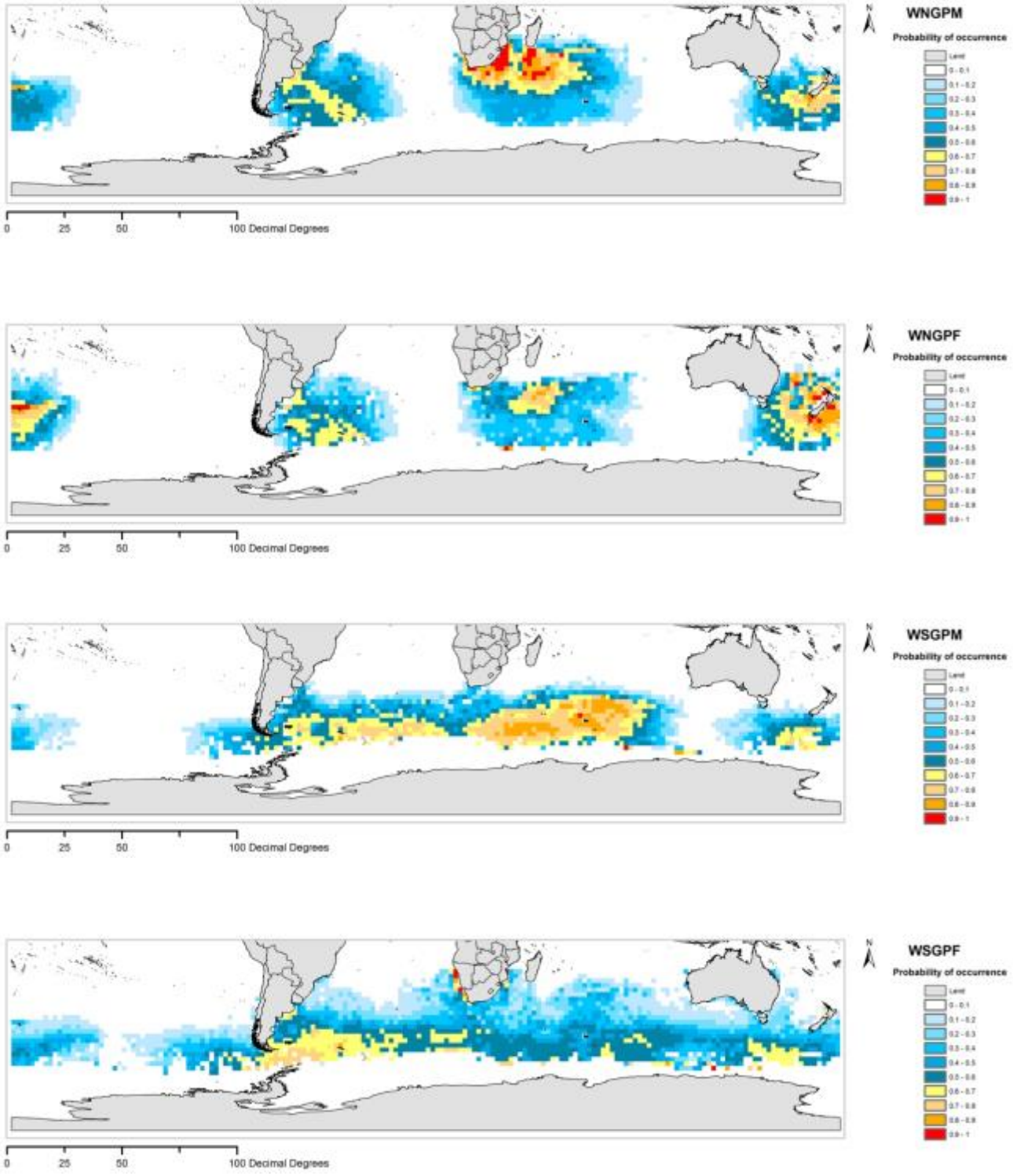

Figure 2 (cont.) - Global predictive distribution maps based on the projection of each seasonal species/sex group model.

Niche overlap metrics (Schoener's D and Levins Niche Breath) are presented on Table 4 and Table 5 respectively.

Table 4 - Niche overlap (using Schoener's D niche overlap metric 0-1) between each group and season.

	SNGPM	SNGPF	SSGPM	SSGPF	WNGPM	WNGPF	WSGPM	WSGPF
SNGPM	1.00	0.67	0.62	0.62	0.66	0.65	0.60	0.67
SNGPF	x	1.00	0.58	0.52	0.75	0.76	0.59	0.59
SSGPM	x	x	1.00	0.69	0.63	0.63	0.75	0.72
SSGPF	x	x	x	1.00	0.61	0.59	0.68	0.78
WNGPM	x	x	x	x	1.00	0.80	0.57	0.60
WNGPF	x	x	x	x	x	1.00	0.55	0.55
WSGPM	x	x	x	x	x	x	1.00	0.72
WSGPF	x	x	x	x	x	x	x	1.00

Table 5 - Niche breadth (using Levins niche breadth metric 0-1) for each group and season.

	B1 (inverse concentration)	B2 (uncertainty)
SNGPM	0.451	0.924
SNGPF	0.365	0.898
SSGPM	0.392	0.906
SSGPF	0.684	0.968
WNGPM	0.397	0.902
WNGPF	0.359	0.890
WSGPM	0.388	0.899
WSGPF	0.591	0.951

Discussion

One of the main challenges in SDM research involves the inclusion of ecologically relevant parameters. Some additional challenges involve the inclusion of migration processes, inclusion of theoretical information from population dynamics, incorporation of interspecific biotic interactions and modelling functional groups of species (Guisan and Thuiller 2005). Our models' results showed to be effective in addressing these tasks. We used presence-only data to generate ecological niche models that (1) describe the seasonal habitat preferences, (2) generate seasonal predictive distribution maps and (3) model the amount of niche overlap.

MaxEnt produced reliable seasonal distribution predictions for the 4 groups, based on datasets with different number of occurrence records. Validation was also satisfactory, given the large amount of test data available for each group. Both Training and Test AUC scores were considerably high for every model, suggesting a good predictive performance in every case.

The coarse spatiotemporal scale approach used in our study may obscure relationships with oceanographic features at a small scale, for instance those related with productivity, such as moving SST fronts or rich water masses. However, this is unlikely to significantly affect our modelling exercise, since seabird numbers are generally influenced by large scale current systems and oceanographic features (Shealer 2002, Newton 2003).

Overall, summer ecological niches clearly reflect the fact that both species are central place foragers. During the breeding season, giant petrels must return to colony to change incubation shift or to feed the hatchlings during guarding and post-guarding period. In these periods, male and female giant petrels share duties and alternate foraging trips that can last from 1 to 30 days. Several studies show that at this time birds have the highest land-based activity, but also travel hundreds or thousands of kilometers to feeding areas.

Logically this is reflected on predictive maps, which show high-probability of occurrence areas centred on colonies.

Giant petrels' summer distribution seems to be strongly constrained by the proximity to breeding colony. This is corroborated by the fact that the most important variable affecting all modelled summer distributions is distance to the breeding colony. The variables dist_seals and dist_cpeng also seem to be relevant to all summer models, and have higher training gain than both chla and sst (usually related with productivity). These results support the idea that during breeding season both species and sexes depend greatly on carrion availability. Though, González-Solís et al. (2007) suggested that intersexual differences in the exploitation of food resources seem greater than interspecific ones: during incubation males feed mainly on penguin and seal carcasses on shore, while females mostly forage at sea. Our results partially agree with this, with SSGPF niche breadth (for Levins metric) being clearly higher than the other groups (B1=0.684). Also, SSGPF predictive maps show the wider high-probability of occurrence areas. However, SNGPF has niche breadth score very similar to SNGPM and SSGPM. Furthermore, intraspecific niche overlap is higher than intersexual overlap.

When comparing both species' summer results, it stands out that SGP have wider high-probability of occurrence areas around colonies and a greater niche breadth than NGP. The winter models present clear evidences of post-reproductive dispersal effects on localization of high-probability of occurrence areas, reflecting a latitudinal segregation between species. During wintering, NGP males and females high-probability of occurrence locations are in northern areas near coast, continental shelf and shelf break. On the other hand, wintering SGP have a higher probability of occurrence on southern latitudes. Despite easy access to foraging habitats exploited by the other sibling species, SGP seem to prefer intraspecific competition rather than to compete with NGP. In this context, the observed pattern probably arose from differences in their tolerance to the physical environment as well as in their competitive abilities.

Giant petrels are the seabirds with the highest wing loading, even higher than albatrosses (Obst & Nagy 1992, Spear & Ainley 1997), which presumably confers a greater flying capability in strong wind conditions (Spear & Ainley 1998). In particular, southern giant petrels males are heavier than females and than northern giant petrels having a greater wing loading (Pennycuick 1987). This may explain why southern giant petrel males tend to visit southern areas in winter, where particularly strong winds may be disadvantageous for giant petrel females and other large seabird species.

Winter niche breadth scores are very similar to summer scores. This models' results show the fundamental niche and the reduction on SGP might be related with the fact that during winter there is a significant increase on sea ice around Antarctica, thus reducing the potential foraging grounds. Similarly to summer models, there is a higher intraspecific niche overlap than interspecific overlap. When comparing winter and summer Schoener's D results for each group, it is clear that despite the high overlap between seasonal niches (D ranging from 0.66 - 0.78), there is a level of differentiation to be considered. Also, there is an increase in niche overlap between sexes of the same species. This can be explained, because wintering giant petrels usually do not migrate to new areas but tend to disperse to areas similar to those used during the breeding season. However, being free of parental duties, birds usually remain in these areas for longer periods than during the breeding season.

The two species seem to compete and share a common preference for the same environment. However, despite easy access to foraging habitats exploited by the other sibling species, southern giant petrels seem to prefer intraspecific competition rather than to compete with northern giant petrels.

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Chapter 3

From locally extinct to a growing population: the range expansion of Audouin's Gull into Portugal and the use of new habitats outside its traditional breeding range

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Abstract

The occurrence of Audouin's Gull (AG) in Portugal is a recent phenomenon. The species breeds in the southern region of Algarve, specifically in Ria Formosa. In this work we explore the offshore habitat use of GPS tracked Portuguese AG during the breeding season in order to quantify the offshore area which might already be protected under the current Special Protection Area network in Portugal. The species breeding range at Deserta colony was estimated using MaxEnt to develop spatial predictive models. We calculated the percentage of SPA area that covers each level of the estimated Core Area of AG occurrence around the colony. The current protected area as a reduced overlap with all the three Core Area levels selected, resulting in only ca. 4.6 to ca. 8.7% of the area used by the species being currently protected.

Introduction

Range shifts in many different taxa have been widely reported in recent decades (Hickling et al. 2006; Chen et al. 2011). However, opportunities to identify the ecological factors influencing range expansion are rare, particularly at the spatial scales relevant to species-based conservation strategies. Understanding species responses to environmental changes, and particularly shifts in their range size and distribution, is therefore a major current challenge for ecologists and conservationists (Thomas 2010; Guisan et al. 2013).The capacity of species to shift distribution will depend upon the constraints imposed by habitat quality and availability, and the consequences for population growth and conservation will depend on the fitness benefits associated with the occupation of new sites (Sutherland 1996). Model systems therefore require well-quantified range changes and the capacity to track individuals in space and time.

The marine environment currently experiences fast climatic change most noticeably in key parameters such as Sea Surface Temperature (Brierley & Kingsford 2009). This is likely to influence how organisms distribute themselves, with those species able of doing so, potentially expanding or shifting their ranges to areas previously unoccupied. But this habitat is also a very a challenging one regarding the monitoring of species' spatial distribution and until the last decade, very little was known regarding the distribution of even very large animals (e.g. whales). Most spatial information on marine animals was gathered by at sea surveys of direct observation or by tag recovery from fisheries or dead recoveries on the shore, which incurred high levels of spatial uncertainty and temporal biases. Recent advances in tracking technology, specifically the miniaturization of data loggers and transmitters have since allowed individual level tracking of most marine animal groups, with seabirds being no exception (Croxall et al. 2005). In fact, developments aimed at seabird tracking have revolutionized tracking technology and devices such as Geolocators are currently used for individual tracking on other avian systems, e.g. shorebirds, passerines (Stutchbury et al. 2009, Conklin et al. 2010), even when positional errors of Geolocators range between 100-200 km (Phillips et al. 2004, Clark et al. 2010).

Current technology offers GPS precision tracking with very light devices, allowing to research space use even of small seabird species, some of which with documented changes on their distribution ranges, as in the case of Audouin's Gull *Larus audouinii*.

Currently, the Audouin's Gull (AG) has a global conservation status of Least Concern (BirdLife International 2015). This species breeds in Spain (19 461 breeding pairs) - mainly the Chafarinas Islands and the Ebro Delta with the later holding 67% of the global population (14 177 in 2007 (Gutiérrez & Guinart 2008), Algeria (100-600), Greece (350-500), Italy (1 153-1 286; Sardinia and Tuscan archipelago), having smaller colonies in Portugal (400-460), France (82; Corsica), Cyprus (14-28), Croatia (60-70), Turkey (47-90; islets and rocks in the southern Adriatic Sea near Korcula and Peljesac Peninsula),Tunisia (70-115) and Morocco (50-300) (all data for breeding pairs, BirdLife International 2015). It winters along the coasts of North and West Africa from Libya to Morocco and along the Atlantic coasts of Africa in Mauritania, Gambia, Senegal and Gabon (Sanpera et al. 2007), with a small wintering population in the eastern Mediterranean along the Aegean coast of Turkey (BirdLife International 2015).

Current global population trend (most of it quantified in Europe and encompassing over 90% of the entire species population), is considered stable or increasing (Barov & Derhé 2011). This is thought to be mainly the result of increased availability of efficient protected areas during the 1980s, and also of discarded fish from trawlers. The effect of discarded fish was observed around the Ebro Delta (Criado 1997; Cama et al. 2013), where the colony has grown rapidly since 1981 (Gutiérrez & Guinart 2008). The large growth of this species in the western Mediterranean has likely caused the breeding population expansion into other locations both inside the Mediterranean, with new colonies found in Croatia, and also one outside the Mediterranean, in southern Portugal (Birdlife International 2004). The occurrence of AG in Portugal is therefore a recent phenomenon (Catry et al. 2010), with the species being considered to be threatened and classified as Vulnerable nationally, mostly due to the low numbers of breeding pairs (Cabral et al. 2005). The species breeds in the southern region of Algarve, specifically in Ria Formosa. Current population is estimated

at 1 200 nesting pairs (J. Ramos, *pers. comm.*), following an initial colonization event recorded in 2002 (Leal & Lecoq 2005). Although this recent colonization was most likely due to immigration of individuals from Spanish colonies, this can be considered as a fragmented subpopulation, given the high degree of isolation in relation to the most important breeding colonies (Cabral et al. 2005). In addition, individuals breeding in Portugal are the first recorded out of the species traditional Mediterranean breeding range (Equipa Atlas 2008).

Here we explore the offshore habitat use of GPS tracked Portuguese Audouin's Gull during the breeding season in order to: (1) model the species habitat used based on environmental variables; and (2) quantify the offshore area which might already be protected under the current Special Protection Area network in Portugal for this species.

Methods

GPS tracking

Between early May and late June 2015, 6 adults and 7 juvenile Audouin's Gulls were captured on nests and tagged with GPS/GSM dataloggers (Movetech/Fleetronic devices), at Deserta Island colony (36.963576°, -7.887174°), in Ria Formosa, southern Portugal. The devices were equipped with high efficiency micro-solar panels to recharge the batteries and allow long-term remote tracking. The electronic equipment was sealed with transparent heat-shrink tube providing resistance to salt water. The devices were attached to the back of the birds using a backpack system with chest harness, which has been previously used in tracking studies with this and another sibling species elsewhere (Camphuysen et al. 2012; Bécares et al. 2015) and proven to be effective and safe for this species. The weight of the sealed devices plus the harness varied between 20 and 24g (depending on the battery capacity used), roughly representing 3–5% of the bird's body mass. The dataloggers were set to perform 15s wake-ups every 30 minutes. During the wake-up, location (Latitude/Longitude), instantaneous speed (m/s) and altitude (m) were registered. GSM connection was set to every 6 hours with data being automatically downloaded from the datalogger to a remote webserver, whenever GSM connection was successfully established. Devices were programmed with a bootloader firmware, to prevent battery damage due to under or over charging. This firmware automatically controlled the device operation, whenever battery voltage was under 3,8V (switching it off until recharge) or above 4,1V (switching it on until battery voltage decreased).

Environmental variables for Spatial Distribution Modelling

When developing Spatial Distribution Models (SDMs), the potential for overfitting increases with model complexity (Franklin 2010), we decided to include in this analysis the minimum number of eco-geographical variables (EGV) considered relevant to explain species distributions (Table 6).

The Digital Elevation Model (DEM) was obtained from the National Geographical Data Center from U.S.A. (ETOPO2; http://www.ngdc.noaa.gov/mgg/image/2minrelief.html), and resampled to a spatial resolution of 0.04167°. This also allowed calculating Slope using ArcGIS software. DEM and Slope are topographic variables that are related, at sea, with oceanographic dynamics and productivity (Louzao et al. 2006; Tremblay et al. 2009; Wakefield et al. 2009; Bécares et al. 2015) and, at land, with the altitude above sea level and terrain relief. Available evidence suggest that AG is a coastal species, that doesn't forage too far from shore (Cabral et al. 2005; Catry et al. 2010; García-Tarrasón et al. 2015), hence Distance to coast was also added as explanatory variable. The variable Distance to Coast is provided as a global data set of distances to the nearest coastline and was acquired from http://oceancolor.gsfc.nasa.gov/DOCS/DistFromCoast/. All other distance variables (Distance to the breeding colony, Distance to ports and Distance to Ramsar sites) were calculated as Cost Distance in ArcGIS. Distances of locations at sea were assigned with a positive value and locations at land with a negative one. The ports location and dimension were obtained from http://www.worldportsource.com/ports/MAR.php. Ramsar sites location and information is available at https://rsis.ramsar.org/ris-search/. Distance to ports was selected as variable because AGs are frequently recorded in flocks at fishing ports (García-Tarrasón et al. 2015). Also they often follow fishing boats and the species is known for its dependency on fishing discards (García-Tarrasón et al. 2015). Distance to Ramsar sites was considered to be a relevant variable, because AG use inland wetlands, for example rice fields or salt marshes (Ruiz et al. 1996; Navarro et al. 2010; Roberts et al. 2010; Bécares et al. 2015; García-Tarrasón et al. 2015).

*Table 6 - List of eco-geographical variables considered for modelling purposes (the **units**, the original spatial resolution **oSR**, the temporal resolution **TR** and the **source** of data are presented for each variable).*

Variable	Units	oSR	TR	Source
Digital Elevation Model; *DEM*	meters	1'	Static	http://www.ngdc.noaa.gov/mgg/image/2minrelief.html
Slope; *Slope*	percent rise	1'	Static	Derived from DEM
Distance to coastline; *Dist_coast*	degrees	0.31'	Static	http://oceancolor.gsfc.nasa.gov/DOCS/DistFromCoast/.
Distance to the breeding colony; *Dist_colony**	degrees	0.31'	2015	Calculated using central point.
Distance to ports; *Dist_ports**	degrees	0,31'	2015	http://www.worldportsource.com/ports/MAR.php
Ports; *ports*	Binary categorical variable	4km	2015	http://www.worldportsource.com/ports/MAR.php
Distance to Ramsar Sites; *Dist_RAMSAR**	degrees	0,31'	2015	https://rsis.ramsar.org/ris-search/
Ramsar Sites; ***RAMSAR***	Binary categorical variable			
Chlorophyll Concentration; *CHL_month*	mg/m^3	4km	Monthly	http://oceancolor.gsfc.nasa.gov/
Sea Surface Temperature; *SST_month*	brightness temperature	4km	Monthly	http://oceancolor.gsfc.nasa.gov/
Night Sea Surface Temperature; *NSST_month*	brightness temperature	4km	Monthly	http://oceancolor.gsfc.nasa.gov/

* These variables were excluded from the model due to strong correlation with *Dist_coast*, which is the more generic variable.

In addition, we obtained monthly data, at spatial resolution of 0.04167°, of Sea Surface Temperature (night and day average), Night Sea Surface Temperature and Chlorophyll Concentration from Aqua-MODIS satellite imagery, available from http://oceancolor.gsfc.nasa.gov/. Extraction and conversion operations were performed

using the Marine Geospatial Tools (MGET) for ArcGIS, an open-source collection of geoprocessing tools for marine research (Roberts et al. 2010). Sea Surface Temperature and Chlorophyll *a* concentration are considered to directly reflect ocean productivity and food availability. Night Sea Surface Temperature was included in the variables list, due to the reported AG's nocturnal foraging habits (García-Tarrasón et al. 2015 and Rodrigues 2015, *unpublished data*). All variables were resampled to the coarsest spatial resolution (0.04167°), using a geographic coordinate system in WGS-1984 datum. We compared models results including different sets of predictive variables and evaluated which had better predictive performance. In order to identify and eliminate strongly correlated variables ($|r|>0.7$) prior to the modelling process, ENM Tools software was used to conduct a Pearson Correlation test (Warren et al. 2010) (Supplementary Material A).

Modelling procedures

Model training and testing was performed with MaxEnt software. MaxEnt is one of the most widely used modelling packages, most likely due to: (1) is one of the most practical methods for modelling species distributions; (2) it typically outperforms other algorithms based on predictive accuracy; (3) it requires only presence data plus environmental information for the entire study area. Thus, MaxEnt is a very useful solution to analyse tracking data, given it only provides information about species occurrence. Detailed description of the MaxEnt and its mathematical computations are given in Phillips et al. (2006), Elith et al. (2010) and Merow et al. (2013). We set MaxEnt to remove duplicate presence records from the same grid cell to minimize autocorrelation biases. The functional forms (known as "feature types") selection was set to the default option "Auto Features".

To account for the effects of geographical sampling bias in the acquisition of data, we produced separate sampling bias grids for each monthly tracking dataset using SDMtoolbox for ArcGIS. This tool creates a bias file for coordinate data (BFCD, downloadable from www.sdmtoobox.org) that is clipped to the size of the study area and then constrained to

a buffered area around occurrence points. This file accounts for background and pseudoabsence sampling biases associated with latitudinal changes in the area encompassed by decimal degree units and it can be used as a bias file in MaxEnt. This inequality results from convergence of the meridians. The BFCD allows equal sampling of background throughout the landscape in geographic projections (Syfert et al. 2013; Brown 2014).

The area under the receiver operating characteristic curve statistic (AUC) was used to test each model's discriminative ability. The Jackknife test of variable importance was used to evaluate the relative importance of each predictor variable considered on each model. The training gain is calculated for each variable alone, as well as the drop in training gain when the variable is omitted from the full model (Peterson et al. 2007; Phillips 2008a). The relative importance of each variable was also analysed, as well as the variables response curves (details in Syfert et al. 2013). Model evaluation was done by cross-validation, randomly splitting occurrence data into a number of equal-size groups (folds) and models are trained leaving out each fold in turn. This approach has a big advantage, which is using all data for evaluation (Phillips et al. 2006; Phillips 2008b).

Niche Overlap

We measured the similarity in predictions between all pairs of SDMs produced by quantifying the niche overlap. We used ENMtools software to calculate the Schoener's D statistics (Warren et al. 2008). It ranges from 0 to 1, with zero indicating no niche overlap between model solutions and one indicating identical predicted distributions.

Core Area definition

To define a core area of AG occurrence around the breeding colony, based not only on tracked locations but also on environmental predictors, we used the averaged overall model to select areas with aggregated cells (at least 3) having a mean logistic value higher than 0.5, 0.6 and 0.7. We used ArcGIS 10.3 to plot contour lines and obtain vector layers for these three Core Area levels. We then compared the results with the present spatial coverage of the Portuguese SPA network, to analyse potential conservation implications. We calculated the percentage of SPA area that covers each level of the estimated Core Area and the percentage of Core Area already under SPA designation.

Results

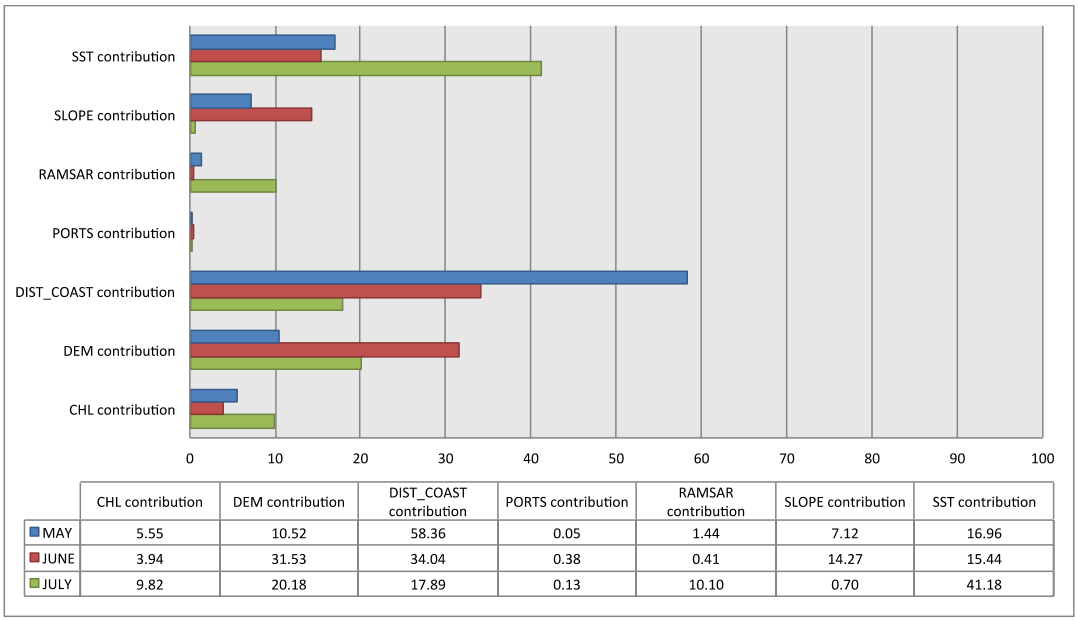
Model evaluation and variables contribution

All three monthly SDMs showed a good (0.9>AUC > 0.8) to excellent (AUC > 0.9) ability to predict the habitat used by the AG, during the breeding season (Table 7).

Table 7 - Training AUC, AUC Standard Deviation (SD) and Test AUC values resulting from model evaluation and cross validation.

Monthly Model	Training AUC	AUC SD	Test AUC
May	0,8804	0,0324	0,8429
June	0,8630	0,0335	0,8176
July	0,9005	0,0364	0,8674

The most relevant variables to the monthly models (Figure 3) were *Dist_coast* (May and June) and *SST_month* (July), with both variables negatively influence probability of occurrence (variables response curves included Supplementary Material B).



	CHL contribution	DEM contribution	DIST_COAST contribution	PORTS contribution	RAMSAR contribution	SLOPE contribution	SST contribution
MAY	5.55	10.52	58.36	0.05	1.44	7.12	16.96
JUNE	3.94	31.53	34.04	0.38	0.41	14.27	15.44
JULY	9.82	20.18	17.89	0.13	10.10	0.70	41.18

***F**igure 3 – Variables' percent contribution to each monthly model. The importance of each variable for each monthly SDM is also given by the corresponding percent contribution value.*

Predictive Distribution Maps

Models show a similar pattern of probability of occurrence between the three months of the breeding season (Figure 4). There seems to be a consistency in terms of spatial use during incubation (May) and chick-rearing periods (June and July). The areas with higher probability of occurrence values are very similar in the three monthly models solutions. This fact is also reflected in the Schoener's D statistics (Table 8), which indicates high niche overlap for every pairwise comparison (ca. 0.8). Thus, a monthly average distribution map was calculated in order to obtain robust breeding season potential area of occurrence around the breeding colony.

Table 8 – Niche overlap using Schoener's D statistic test. Index values range from 0 (no overlap) to 1 (identical areas).

	May	**June**	**July**
May	1.00	0.830	0.794
June	-	1.00	0.790
July	-	-	1.00

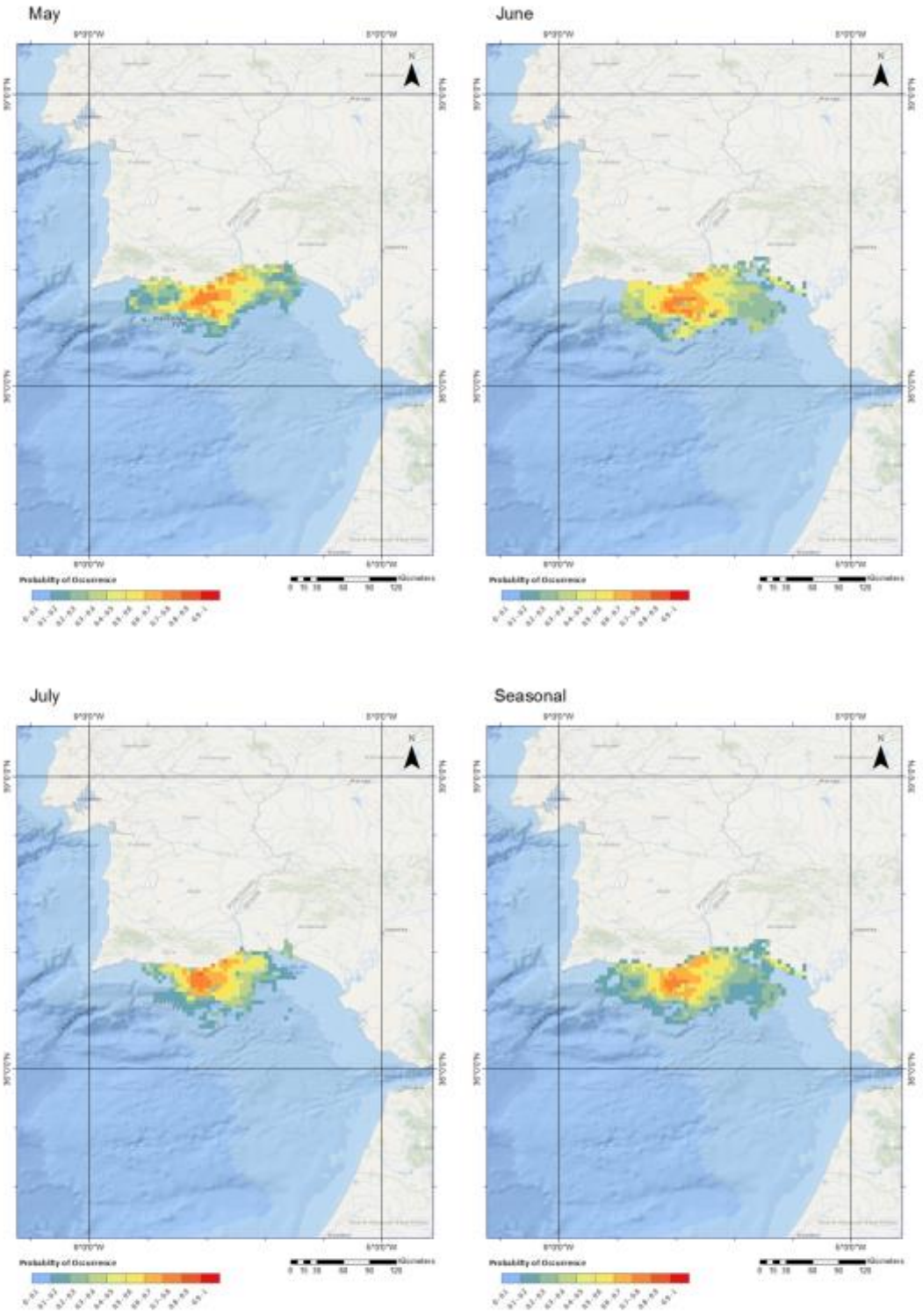


Figure 4 - Predictive distribution maps of breeding Audouin's Gulls in southern Portugal. Monthly probabilities of occurrence (May-July) were averaged, resulting on an overall map. Probability of occurrence is reflected in a logistic output scale varying between 0 and 1.

Core Area protection level

Core Area protection levels are defined by 3 contours 0.5, 0.6 and 0.7, based on the averaged overall model (Figure 5). The estimated Core Area only overlaps with one SPA (Figure 6), Ria Formosa (PTZPE0017). Therefore, the "SPA total area", used to calculate percentage of overlap with Core Area contours, only considers this site (23269ha).

The proportion of each Core Area level and SPA under the overlap zone represent, both the proportion of each Core Area level already designated as SPA (from ca. 8.7 to 4.6%) and, the proportion of SPA that already protects each Core Area level (from ca. 69 to 3.5%) (Table 9 *–SPA percent overlap with the 3 Core Area levels, and percentage of each Core Area included in the SPA.*).

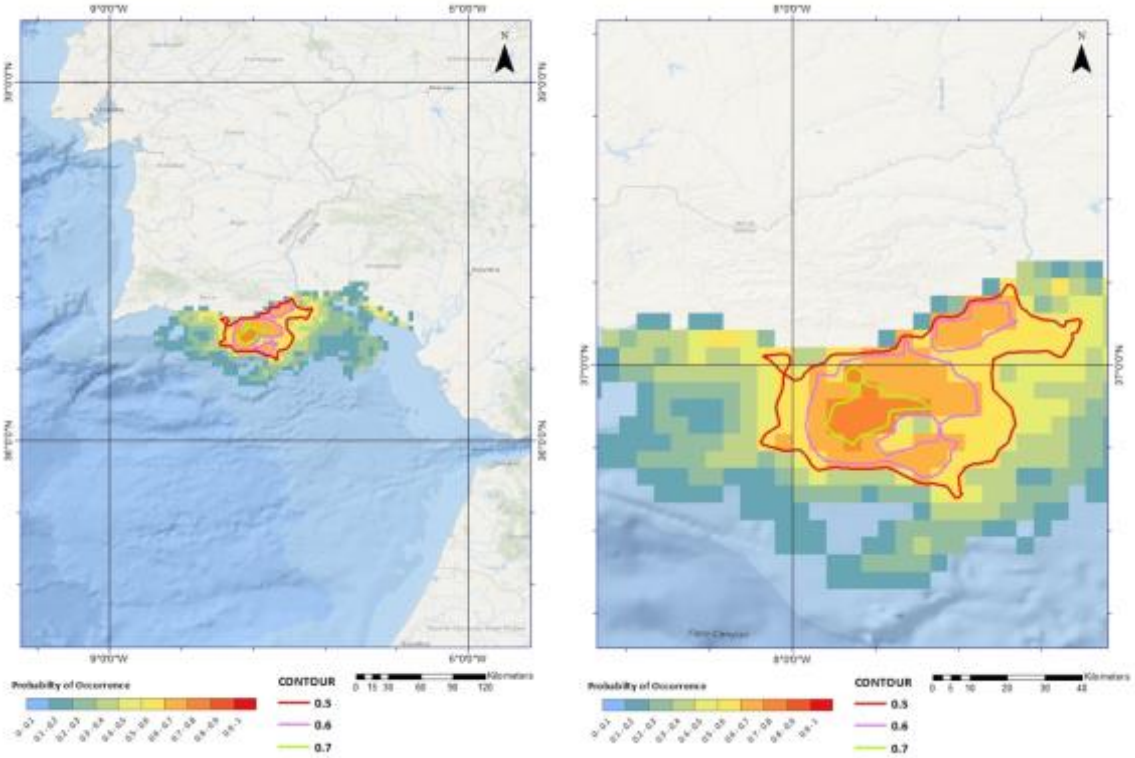


Figure 5 - Core Area contours with low (left) and high (right) image zoom. Contour lines are shown to each Core Area level (red – 0.5; purple – 0.6; green – 0.7), based on the averaged overall model (probability of occurrence between 0 and 1).

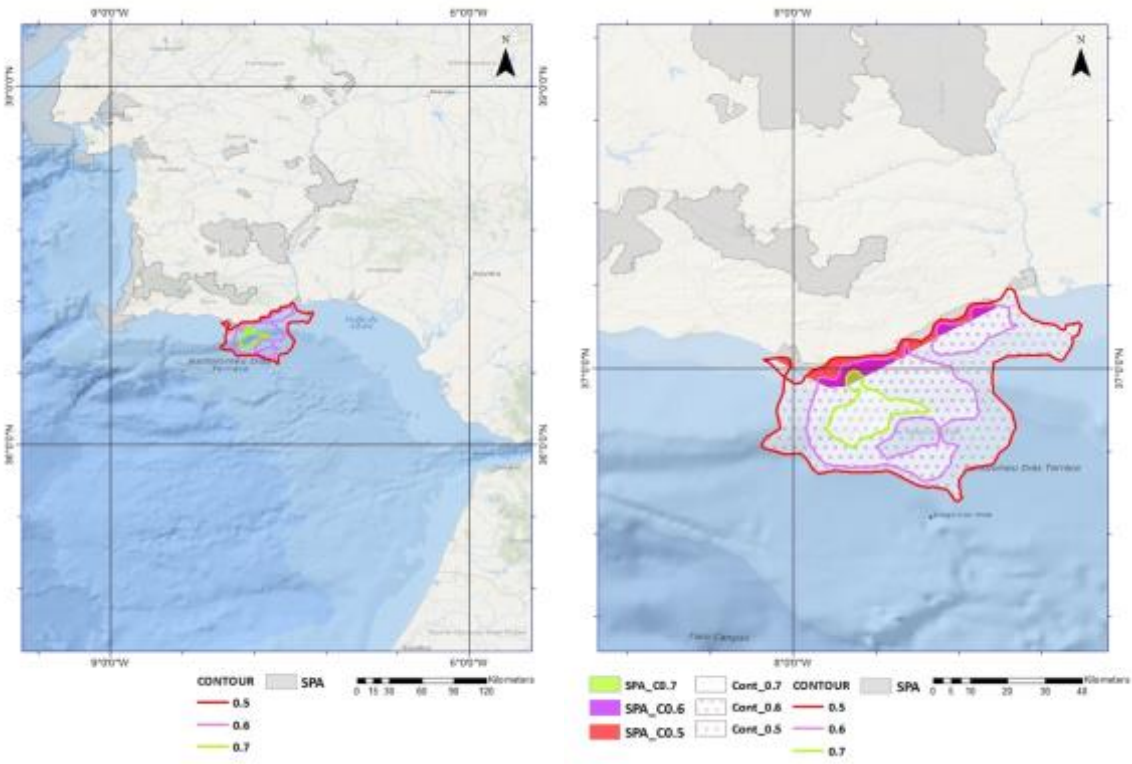


Figure 6 – Overlap between Core Area and SPAs with low (left) and high (right) image zoom. Contour lines delimit polygons of the different Core Area levels. The overlap zones between these polygons and SPAs are shown with filled colour.

Table 9 –SPA percent overlap with the 3 Core Area levels, and percentage of each Core Area included in the SPA.

	SPA_CONT_0.5 Overlap	**SPA_CONT_0.6 Overlap**	**SPA_CONT_0.7 Overlap**
SPA (% Total Area)	69.2%	25.0%	3.5%
CONT_0.5 (% Total Area)	8.7%	-	-
CONT_0.6 (% Total Area)	-	6.2%	-
CONT_0.7 (% Total Area)	-	-	4.6%

Discussion

Audouin's Gull breeding in Portugal do not visit the species' traditional foraging areas in the Mediterranean during breeding season, neither on other periods (Rodrigues 2015, *unpublished data*). This is a particularly interesting result as the Portuguese population is most likely an extension of the Spanish, which has its stronghold in Ebro Delta, hosting more than two thirds of the entire breeding population (BirdLife International 2016). Population growth and expansion to new locations is attributed to the increased availability of fisheries discards close to key breeding colonies, particularly in the Ebro Delta where waste from the trawlers is not used industrially to produce food for domestic animals, as occurs in other areas, and its rather discarded near the colony (Gutiérrez & Guinart 2008). Fishing discards and the creation of protected areas in the 1980s are regarded as the main causes for the population recovery (Criado 1997), which increased from only 1000 pairs in 1975 to 21 161 in the present and current population is stable or increasing (Gutiérrez & Guinart 2008; Barov & Derhé 2011). In Portugal however, and despite the very costal distribution of the species, the current protected area has a reduced overlap with all of the three Core Area levels selected, resulting in only ca. 4.6 to ca. 8.7% of the area used by the species being currently protected.

The use of new GPS/GSM technology provided good results, likely due to the proximity to areas with good GSM cover in coastal Algarve (South Portugal). Tracking data was thus of good quality and frequency allowing to create good predictions of occurrence using MaxEnt and based on the selected environmental variables. For all breeding months AUC values based on the tracking dataset (using 10 folds of the empirical tracking dataset to replicate monthly model calculations) were above 0.8 providing high confidence estimates of AG occurrence (Syfert et al. 2013). The variables that most contributed to the monthly models were *Dist_coast* (May and June) and *SST* (July) (Figure 3). *Dist_coast* is strongly correlated

with the excluded variable *Dist_colony* and it is reasonable to assume that this variable reflects the species coastal behaviour, as well as, the limited foraging range in close proximity to the colony location, especially during incubation. SST is a proxy for productivity that contributes considerably when adults are in the later stages of chick-rearing period (July). Bécares et al. (2015) in the Mediterranean found that *Dist_colony*, *Dist_ports* (both negatively affecting occurrence probability), *CHL_month* and *SST_month* were the most relevant variables on their predictive models of AGs foraging habitats. Those models were based on a larger set of environmental and ecological variables (16 in total), indicating that albeit being in a recently occupied location this species relies on the same environmental predictors as on the traditional colony with the exception of *Ports*, which is of little relevance in Portugal. This may be due to the fact that we used a binary variable in our models to avoid correlation between distance variables. It may be also due to ecological differences in both areas, since Spanish ports have large fishing fleets whereas this is not the case in Portugal and potentially aggravated by the fact that AGs in the Portuguese colony are yet to learn how to explore the discards in the vicinity of ports (see below). Also, trawl fleet in Algarve region is relatively small and is mostly concentrated in Portimão harbour (about 60km away, in straight line, from the colony). Purse seine and polyvalent fleets (that operate on the other ports of Algarve) do not generate large amount of discards and offal, as the trawl fleet does. This way AG might feel more attracted to areas where trawlers operate, along the continental shelf break. Conversely, *DEM* and *Slope* contributed considerably on our predictive models but not in the Mediterranean (Bécares et al. 2015). Distinct bathymetry between the two foraging areas can potentially justify these differences, as depths in costal Mediterranean (a mostly inland sea) are much lower and vary less in slope than in the Portuguese Atlantic coast. Regardless of the methodological and fine differences between these studies, both highlight the overwhelming contribution of distance to colony or coast and productivity for predicting this species distribution during breeding season.

The absence from Mediterranean waters of Audouin's Gull breeding in Portugal indicates that these individuals are not dependent on the traditional foraging areas of this species. This has occurred in a relatively short time (generation length estimated by BirdLife International to be 13 years, BirdLife International 2016), as the colony has only 13 years, indicating that colonizer individuals likely started using new foraging grounds as early as settlement occurred. Furthermore, it indicates that this thriving breeding population is independent from the local scale fluctuations recorded in the Spanish colonies (Barov & Derhé 2011). Given the forecasted decline in the unsustainable trawling fishery of the largest colony, the Ebro Delta, (Oro et al. 2004; Tavecchia et al. 2007; Barov & Derhé 2011) and the potential reduction of small pelagic fish stocks due to increasingly high fishing pressure around the Mediterranean breeding grounds, owing partly to high demand of fish feed from tuna-farming (Arcos et al. 2008), the Portuguese breeding colony might therefore gain regional relevance in the near future. Although some fish stocks in Portuguese waters are potentially under pressure (sardines, hake, etc.) (ICES 2015a, 2015b), the local AG colony is increasing while others remain stable. This indicates the urgency in projecting protected areas encompassing the species foraging grounds given the current scenario of fishing stock reductions. The Core Area delimitation for the averaged overall model shows the species vital area during breeding season ranked in 3 importance levels for conservation. At the moment this area should be considered as the most important to ensure species conservation in Portugal.

Despite the low spatial variation on distribution during the breeding season, there is a tendency for predicted areas of occurrence to have a wider latitudinal range in May and a wider longitudinal range in June, than in July. This is probably a consequence of the timing of breeding season events, as May and part of June will very much refer to incubation, when both adults can do larger trips from the colony to feed themselves, whereas July will mostly encompass chick rearing phase, when regular feeding of small food items is required, likely keeping adults at short distances from the colony (Mañosa et al. 2004; Burger et al. 2016). However, and given that the Schoener's *D* statistic revealed very high

niche overlap between the breeding season months these were all averaged into one (Warren et al. 2008). This is also supported by the need to protect areas used throughout the breeding season given that selecting only one stage (or month) of this period could result in decreased fitness. For example, if only offshore areas used during late incubation in June are protected, then unprotected coastal sites important during chick rearing could potentially result in low feeding rates and consequent depressed chick development and even pre-fledging mortality (Vigfusdottir et al. 2013). It is therefore important to plan integrated conservation areas ensuring that all stages of the breeding season are accounted for.

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Chapter 4

Designing offshore EU Marine Protected Areas using Spatial Conservation Planning techniques: a case study of the country with the largest European EEZ, Portugal

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Abstract

The purpose of SDMs, and in particular of predictive mapping, is to provide spatially explicit information on species and other elements of biodiversity for conservation planning. In this study, we develop a spatial conservation prioritization for marine birds across mainland Portuguese Exclusive Economic Zone (EEZ), in preparation of eventual future expansion of the current conservation area networks and definition of MPAs, as well as, for the implementation of management plans on currently established SPAs, with particular focus on offshore areas. Our results address many of the conceptual planning needs Portugal has for the marine environment. Some of the identified key areas are located in regions thought to be important for marine biodiversity, due to their environmental characteristics. The final results are also very relevant to undertake in the future best practice management actions.

Introduction

The designation of Marine Protected Areas (MPAs) is currently considered one of the best solutions to ensure the protection of relevant marine species and habitats (Kelleher 1999). In a long-term perspective, and besides its primary aim for the conservation of target species and/or habitats, MPAs can also play an important role in restoration of overharvested and heavily exploited ecosystems. It is therefore essential that the design of MPAs is based upon robust information on species occurrence and spatial distribution, as well as, on the association between that empirical record and oceanographic environmental variables. In the marine environment, the mechanisms that regulate species occurrence are still widely debated. Nevertheless, species occurrence and spatial distribution data of target species are essential for the implementation of management plans, and to evaluate the effectiveness and success of these conservation tools and should thus form the base of MPA design and evaluation procedures.

One of the key challenges that the European Union (EU) biodiversity policy currently faces, is the full implementation of the Natura 2000 network in the marine environment. The implementation of MPAs is often hindered by legal difficulties in defining reserves on international waters, the patchy nature of data in many offshore waters and/or by the scarcity of comprehensive data and studies describing long term biological patterns for multiple species, particularly in offshore waters (Leathwick et al. 2008). Seabirds are relatively easy to monitor offshore as these can be recorded from a boat by direct observation and can be used as a starting point for the mapping of potential MPAs, which might originate from Important Bird Areas (IBA). In the EU, the identification and delimitation of Special Protection Areas (SPAs) for seabirds must be entirely based on scientific criteria, such as the percentage of the population of a priority species under the Birds Directive, although Member States have a margin of discretion in determining the most appropriate criteria (Stroud et al. 2001). In any case, countries must fully apply those criteria in a way that ensures that all the 'most suitable territories', both in number and

surface area, are designated for protection. Based on the information provided by the Member States, the European Commission evaluates if the designated sites are sufficient to form a coherent network for the protection of the vulnerable and migratory species using EU's waters (European Commission 2007).

Between 2012 and 2015, Portugal made an important step towards the implementation of Natura 2000 network in the marine environment, by enlarging and establishing new marine Special Protection Areas (SPAs) for priority species under the Birds Directive (Decree-Law n. 105/2012, Regulatory Decree n. 17/2015 and Decree-Law n. 204/2015). Although, this process was mainly aimed towards the designation of marine SPAs for the conservation of the following species: *Puffinus mauretanicus, Oceanodroma castro*, *Morus bassanus, Melanitta nigra* and *Calonectris diomedea*. Despite being a multi-species approach, most of the rare and non-threatened species were not considered in the analysis, which led to the definition of SPAs only in territorial sea (until 12nm). Consequently, no relevant offshore areas were found to be relevant for designation as marine SPAs. The recent publication of the Portuguese Atlas of Marine Birds (Meirinho et al. 2014) allows now considering all seabird species for the designation of SPAs offshore. This timely Atlas, presents the seasonal distributions of all seabird species that occur on Portuguese waters (Meirinho et al. 2014) and for most of the species it contains seasonal Spatial Distribution Models, based on a large set of environmental predictors, therefore being an useful tool for marine spatial planning and management. Data collection protocols allowed gathering information with a good temporal and spatial resolution encompassing a relatively large study period (December 2004 to December 2012). SDMs were developed using MaxEnt software, which is now considered to be a common SDM tool, as it is very simple to use and is especially efficient in handling complex iterations between response and predictor variables (Elith et al. 2006, 2010; Fourcade et al. 2014).

The purpose of SDMs, and in particular of predictive mapping, is to provide spatially explicit information on species and other elements of biodiversity for conservation planning. Grid-based atlases of species distribution have been widely used to collect data on distribution of different species, especially birds and can be used to obtain information about species-

environment relationships using these type of quantitative models. These studies have the advantage of using systematic methodologies to collect data about species distributions (Franklin 2010), hence the protocols can be replicated at different times, allowing to conduct long term monitoring studies. In recent years a novel approach to developing SDM's has been gaining attention due to its integrative model: Spatial Conservation Planning (SCP). This is a multidisciplinary approach that relies on inputs from several fields, such as spatial ecology, economy, geography or sociology and aims to identify important areas for biodiversity and efficiently achieve conservation goals (Lindenmayer & Hunter 2010; Reyers et al. 2010; Kukkala & Moilanen 2013). One of the most important steps in SCP is termed "spatial conservation prioritization". This step requires the use of decision support systems and planning software, based on complex mathematical algorithms, to identify important areas for conservation or protected network expansion (Pressey & Bottrill 2009; Kukkala & Moilanen 2013). There are several decision support systems and planning software available to select areas with good habitat quality and connectivity. One such software frequently used is Zonation which includes a set of useful features, most noticeably allows for uncertainty analysis, species weighting and seven ways of dealing with connectivity (Lehtomäki & Moilanen 2013).

In this study, we develop a spatial conservation prioritization for marine birds across mainland Portuguese Exclusive Economic Zone (EEZ), in preparation of eventual future expansion of the current conservation area networks and definition of MPAs, as well as, for the implementation of management plans on currently established SPAs. Our approach is based on decision-theoretic and optimization techniques, specifically using Zonation spatial planning software (Lehtomäki et al. 2009; Kukkala & Moilanen 2013). The main innovation in this technique is the multi-specific approach that aggregates seasonal SDMs for a large number of marine bird species occurring on the study area (common, rare, threatened and not-threatened) and the ability to combine these for identifying important conservation areas both offshore, in-shore, seasonally and overall.

Methods

Data Collection

Survey data was collected following the protocols developed for Portuguese Atlas of Marine Birds (for details see Meirinho et al. 2014). In short, from December 2004 to December 2012 ship-board surveys were conducted off the coast of Portugal and western Andalusia, broadly between 34°N and 42°N, and 6°W and 14°W. Most of the survey effort was carried out between March and November of each year, with fewer surveys from December through February. Standard protocols of European Seabirds at Sea data collection were used (Tasker et al. 1984; Camphuysen & Garthe 2004) on board four similar research vessels. All seabirds in contact with water within 300 m of the survey transect were counted on one side of the ship, and all flying seabirds were counted using the 'snap-shot method', with bird observations summed over 5 min periods.

Environmental predictors

To model seabird species distribution, 19 environmental variables were selected (Table 10). These variables are either known, or expected, to be 'usually' correlated with seabird distribution and abundance (e.g. Louzao et al. 2006; Tremblay et al. 2009a, 2009b; Wakefield et al. 2009). The oceanographic data were obtained from Bloom-Watch 180, as remote sensing products (i.e. satellite imagery). Physical variables (e.g. bathymetry) were extracted only once since they are static over the study period. Dynamic oceanographic variables (e.g. Sea Surface Temperature – sst) were extracted as monthly averages, from Aqua MODIS and Pathfinder AVHRR satellite imagery, and varied among seasons and years during the study period.

The effect of environmental variables on ocean productivity is not immediate, as in many cases there is a delay between some oceanographic phenomenon and prey occurrence. In order to account for productivity time lags we integrated Sea Surface (*sst*) and Chlorophyll a Concentration (*chla*) over a period of three months prior to each season: Winter, Spring, Summer and Autumn (Louzao et al. 2009). To account for annual anomalies we included the *sst* and *chla* anomalies (i.e. *asst* and *achla*) for each season, calculated as the difference between the average value for a given season and year and the average for that season over a 20-year period in that grid cell. Given that seabirds may respond to spatial gradients of oceanographic variables (Louzao et al. 2006; Tremblay et al. 2009a; Wakefield et al. 2009), we also calculated spatial *sst* and *chla* gradients as: (maximum value x minimum value) x 100/maximum value; with maximum being the highest and minimum the lowest seasonal mean *sst* or *chla* value over a moving 3 x 3 grid cell window (i.e. 144km^2). This dimensionless metric expresses the magnitude of change in each habitat variable, scaled to the maximum value. The spatial gradients of chlorophyll a (*gchla*) and sea surface temperature (gsst) indicate the presence of frontal systems, whereas the gradient of bathymetry (*gbat*) reflects the presence of topographic features (e.g. shelf break or seamount). Finally, we used the *sla* in each season as an indicator of mesoscale structures that mix additional nutrients up into to the surface layer.

To evaluate the persistence of productive zones in the study area, we used chlorophyll a concentration datasets for the study period. Global persistency was calculated in 2 steps: 1) for any given year, in each seasonal *chla* map (3 months), we identified cells with high nutrient concentration (*chla* > 1 mg m^3); 2) for each pixel, we counted the number of seasonal maps with high nutrient concentration.

Environmental variables considered in the analytical process are shown in Table 10.

Table 10 – List of environmental variables used on species distribution models.

Variable	Data source
Min. Sea surface temperature (sst)	Aqua - MODIS
Average SST (avgsst)	Aqua – MODIS
Maximum SST (mxsst)	Aqua – MODIS
SST Variation (varsst)	Aqua – MODIS
SST anomaly (asst)	Aqua – MODIS
Gradient SST (gsst)	Aqua – MODIS
Distance to SST fronts (dist_sstfrt)	Calculated on R
Sea surface height anomaly (assh)	Satellite AVISO
Min. Chl *a* concentration on sea surface (chla)	Aqua – MODIS
Medium Chl *a* (mdchla)	Aqua – MODIS
Max. Chl *a* (mxchla)	Aqua – MODIS
Chl *a* Variation (varchla)	Aqua – MODIS
Chl *a* anomaly (achla)	Aqua – MODIS
Chl *a* gradient (gchla)	Aqua – MODIS
Distance to Chl *a* fronts (dist_chlafrt)	Calculated on R
High Chl *a* persistence (pchla)	Aqua – MODIS
Mesoscale eddies (sla)	Calculated on R
Bathymetry (bat)	ETOPO 1
Bathymetry gradient (gbat)	ETOPO 1
Distance to line shore (dist_shore)	Calculated on R

Species Distribution Modelling

Data processing and exploratory analysis

All observations were binned into a spatial grid with cell size 4km (0.0417°) to match the spatial resolution of remotely sensed environmental data. Every grid cell received an additional binary detection/non-detection value of '1' (hereafter referred to as 'presence'), whereas grid cells that were surveyed but where no target seabird species were observed were coded as '0' (hereafter referred to as 'absence').

Model construction

Model construction, training and testing was performed with Maximum Entropy (MaxEnt) modelling based on presence-only data (version 3.3.3 (http://www.cs.princeton.edu/~schapire/maxent/ [accessed 18 October 2012]). MaxEnt is a general-purpose method for characterizing probability distributions from incomplete information. In estimating the probability distribution defining a species' distribution across a study area, MaxEnt formalizes the principle that the estimated distribution must agree with everything that is known (or inferred from the environmental conditions where the species has been observed), but should avoid making any assumptions that are not supported by the data. The approach is thus to find the probability distribution of maximum entropy (the distribution that is most spread-out, or closest to uniform) subject to constraints imposed by the information available regarding the observed distribution of the species and environmental conditions across the study area.

The MaxEnt method does not require absence data for the species being modelled; instead it uses background environmental data for the entire study area. The method can use both continuous and categorical variables and the output is a continuous prediction (i.e. a cumulative probability ranging from 0 to 1 that indicates relative suitability).

Model evaluation and calibration

We divided the survey data into training and test datasets by setting aside approximately 30% of the surveyed area for spatial evaluation of the models (Araújo & Guisan 2006). We first ran MaxEnt on the presence-only positions 100 times and then calculated the mean of the 100 MaxEnt predictions, to obtain an average prediction and coefficient of variation of those predictions. MaxEnt program was run separately for different species and seasons (i.e. winter, spring, summer, autumn). The settings were: logistic output format, resulting in values between 0 and 1 for each grid cell, where higher values indicate more similar climatic conditions; duplicates removed; and 100 replicate runs of random (bootstrap) subsamples with 30 as random test percentage. The results were summarized as the average of the 100 models. There are three main results of MaxEnt; jackknife chart, Receiver Operating Characteristics Curve (ROC) and probability map. Jackknife chart was used to evaluate the contribution of each environmental layer to the final result, thus providing the explanatory power of each variable when used in isolation. The ROC curve describes the model's accuracy measured by the Area Under the ROC Curve (AUC). The AUC estimates the likelihood that a randomly selected presence point is located in a raster cell with a higher probability value for species occurrence than a randomly generated point (Phillips et al. 2006). Generated models are generally interpreted as excellent for test AUC > 0.90, good for 0.80 < AUC < 0.90, acceptable for 0.70 < AUC < 0.80, bad for 0.60 < AUC < 0.70 and invalid for 0.50 < AUC < 0.60 (Araújo et al. 2005). All model evaluation statistics and optimal thresholds were calculated using the package 'PresenceAbsence' in R 2.15. (R Development Core Team 2012). Finally, the probability map shows the spatial distribution of predicted presence probability and is used for graphical representation of the distribution data.

Spatial prioritization

In the second phase of this analysis, we used Zonation 4.0.0 to perform a spatial prioritization analysis, based on statistical seasonal seabird distributions models, to identify relevant marine conservation areas. Zonation is based on the specification of priorities and connectivity responses for biodiversity features (Moilanen 2007; Leathwick et al. 2008).

Zonation algorithm starts by assuming that the full landscape is protected, and proceeds by progressively identifying and removing cells that cause the smallest marginal loss in conservation value. Low conservation cells are removed first, leaving high conservation grid cells to last, which correspond to the important conservation areas (Moilanen 2007; Moilanen et al. 2014). The first and most important part of the analysis is the meta-algorithm selection, which will define the marginal loss. Here, we used the Core Area Zonation (CAZ) meta-algorithm. CAZ aims to ensure high-quality locations for all species, including those that occur in otherwise species poor areas (Leathwick et al. 2008; Lehtomäki & Moilanen 2013). Therefore, CAZ it is able to identify as high-priority areas that have a high occurrence level for a single rare and/or highly weighted feature (Minin et al. 2014). Succinctly CAZ uses the following principles: (1) of two otherwise equal locations, that with a lower occurrence for the most important species is removed first; (2) assuming two otherwise equal locations, that with the occurrence of a lower-weight species is removed before that with an equal occurrence for a high-priority species; (3) assuming two identical locations with identical original occurrence levels for two different species, the one retained is that which contains a species that has lost more of its distribution; (4) of two otherwise identical locations, that with higher cost is removed first (Moilanen 2007; Leathwick et al. 2008; Moilanen et al. 2014).

Species were assigned with different priority weights, based on their national conservation status (Table 11) and their phenology in the study area (Table 12). We attributed a score to each of the categories of these 2 criteria, as shown in. For each species, overall weights were calculated by multiplying the 2 scores (Supplementary Material C).

Table 11 - Conservation status categories and attributed scores for calculation of zonation species weights.

Conservation Status	Attributed weight
Least Concern (LC)	1
Near Threatened (NT)	1,5
Vulnerable (VU)	2
Endangered (EN)	3
Critically Endangered (CR)	4

Table 12 - Phenological status categories and attributed scores for calculation of zonation species weights.

Phenological Status	Attributed weight
Visitor / Winter Visitor	1
Migratory reproductor	1,5
Reproductor	2
Resident	3

Methods for reserve selection and conservation planning often ignore uncertainty. For example, presence-absence observations and predictions of habitat models are used as inputs but commonly assumed to be without error. But zonation provides an uncertainty analysis feature aiming at robust conservation decisions (Moilanen et al. 2006b, 2014). Uncertainty analysis provides a consistent framework for understanding potential consequences of errors in inputs and achieve a given conservation target, despite uncertainty in data. Zonation applies one particular branch of decision theory, information-gap theory, to conservation planning based on probabilities of occurrence. The underlying method is the "distribution discounting", in which the site- and species-specific measure of conservation value (related to species-specific occupancy probabilities) was penalized by an error measure (in our study, related to accuracy of statistical prediction) (Moilanen et al. 2006a, 2006b).

For each seasonal species distribution model, a corresponding uncertainty map was calculated on MaxEnt. These uncertainty layers represent the Standard Deviation (SD) of the probability of occurrence estimates.

We selected Zonation to perform a spatial priority rank analysis for each season (Spring, Summer, Autumn and Winter). The informative layers used in this spatial analysis include, for each season, a total of 34 (Spring), 22 (Summer), 34 (Autumn) and 20 (Winter) seasonal species predictive and uncertainty maps obtained with MaxEnt (seasonal species maps are available online at http://www.atlasavesmarinhas.pt/ for detailed information on species occurrence).

We carried out four analyses that identified seasonal high priority conservation areas for seabirds across mainland Portugal. The spatial area considered for this study includes the continental Portuguese EEZ (offshore area), territorial and interior waters (inshore area). We then used the seasonal results to identify high priority offshore areas for seabird conservation, by extracting the results using an offshore area mask. We then combined the 4 seasonal solutions in a mosaic raster by selecting the blend option in ArcGIS 10.3 mosaic to new raster tool.

To identify the best offshore areas for seabird conservation, we selected the 10% Top Fraction of the combined final solution. According with Lehtomäki & Moilanen (2013) the best top fraction values to identify the best areas for conservation typically varies between 2% and 20%. We selected an intermediate value in this range that outputted satisfactory results and ensures that these areas contain a balanced representation of all features (habitat type and/or species distributions) included in the analysis (Kremen et al. 2008; Lehtomäki & Moilanen 2013).

Results

The generic results allowed to identify four seasonal high priority conservation areas for seabirds across mainland Portugal. The seasonal results are presented in priority rank maps, shown in Figure 7. For better visualization of seasonal results, the four maps show the wider distribution of the best areas for conservation identified by the highest-ranked cells in the 20% top fraction. These generic results are the baseline analysis, based on seasonal multispecies distribution datasets and on a well supported analysis parameterization which accounts for predictive uncertainty.

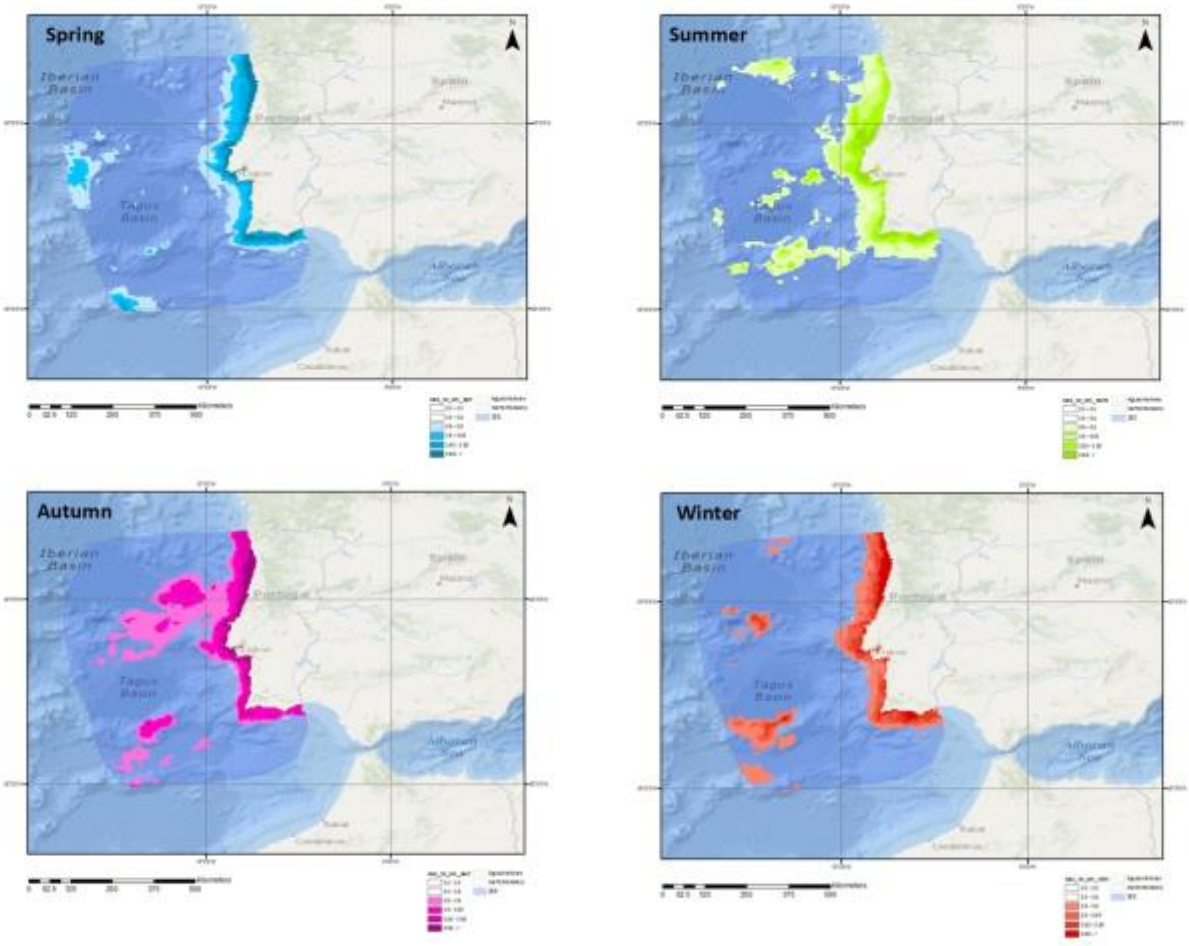

Figure 7- Seasonal high priority areas for seabirds across mainland Portugal. Spatial prioritization results for offshore area and inshore area obtained using Zonation. High priority levels shown include the 20%, 10% and 2% Top Fractions.

Offshore areas with high conservation value were identified using the baseline analysis results. Figure 8 shows the seasonal relevant offshore areas, identified by the 20% Top Fraction.

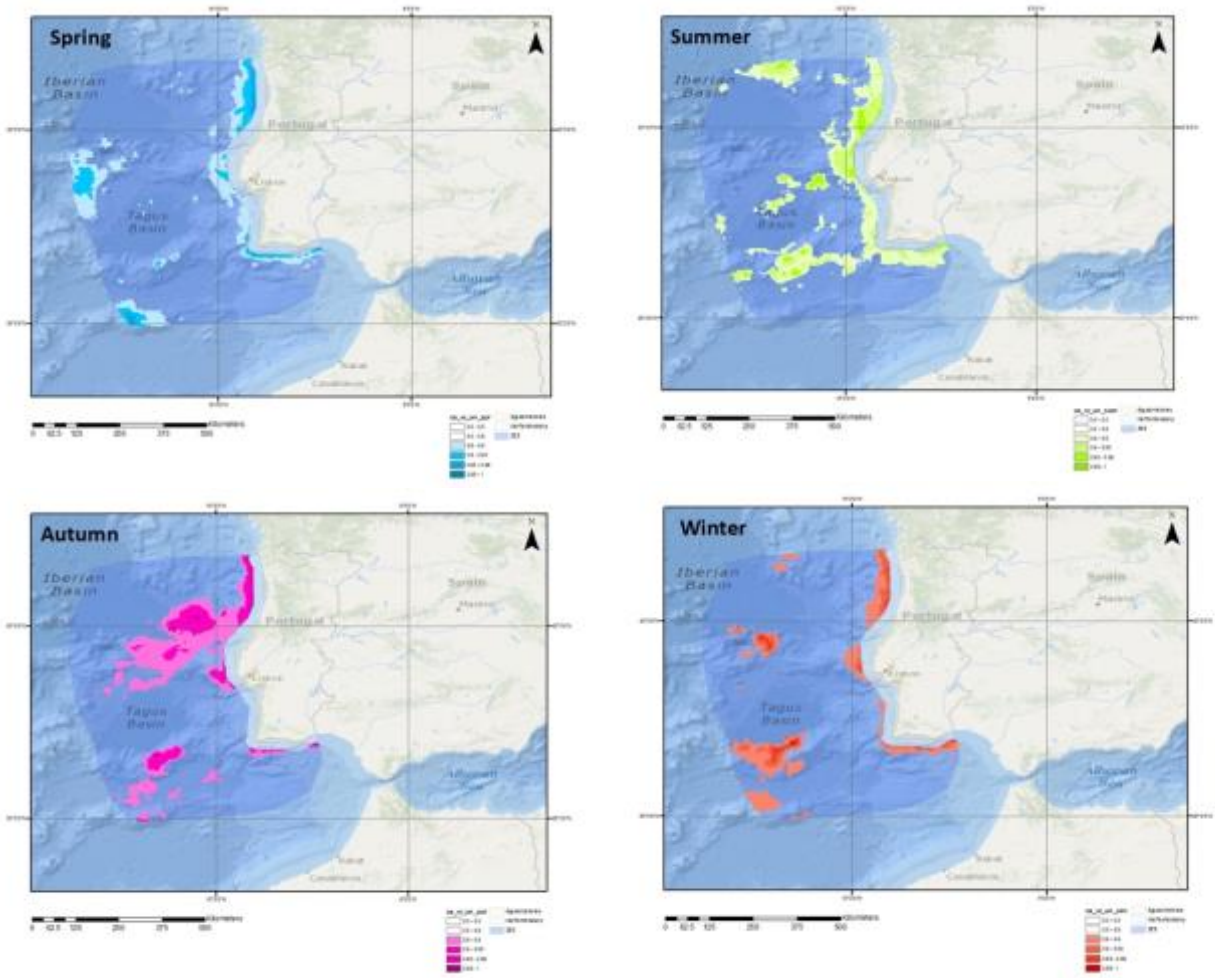

Figure 8 - Seasonal high priority offshore areas for seabirds across mainland Portugal. Spatial prioritization results for the offshore area obtained using Zonation. High priority levels shown include the 20%, 10% and 2% Top Fractions.

Figure 9 is the map for the final solution of offshore conservation area selection. This figure presents the result of the combination of all 4 seasonal offshore areas. The output cell value of the overlapping areas is a horizontally weighted calculation of the values of the cells in the overlapping area.

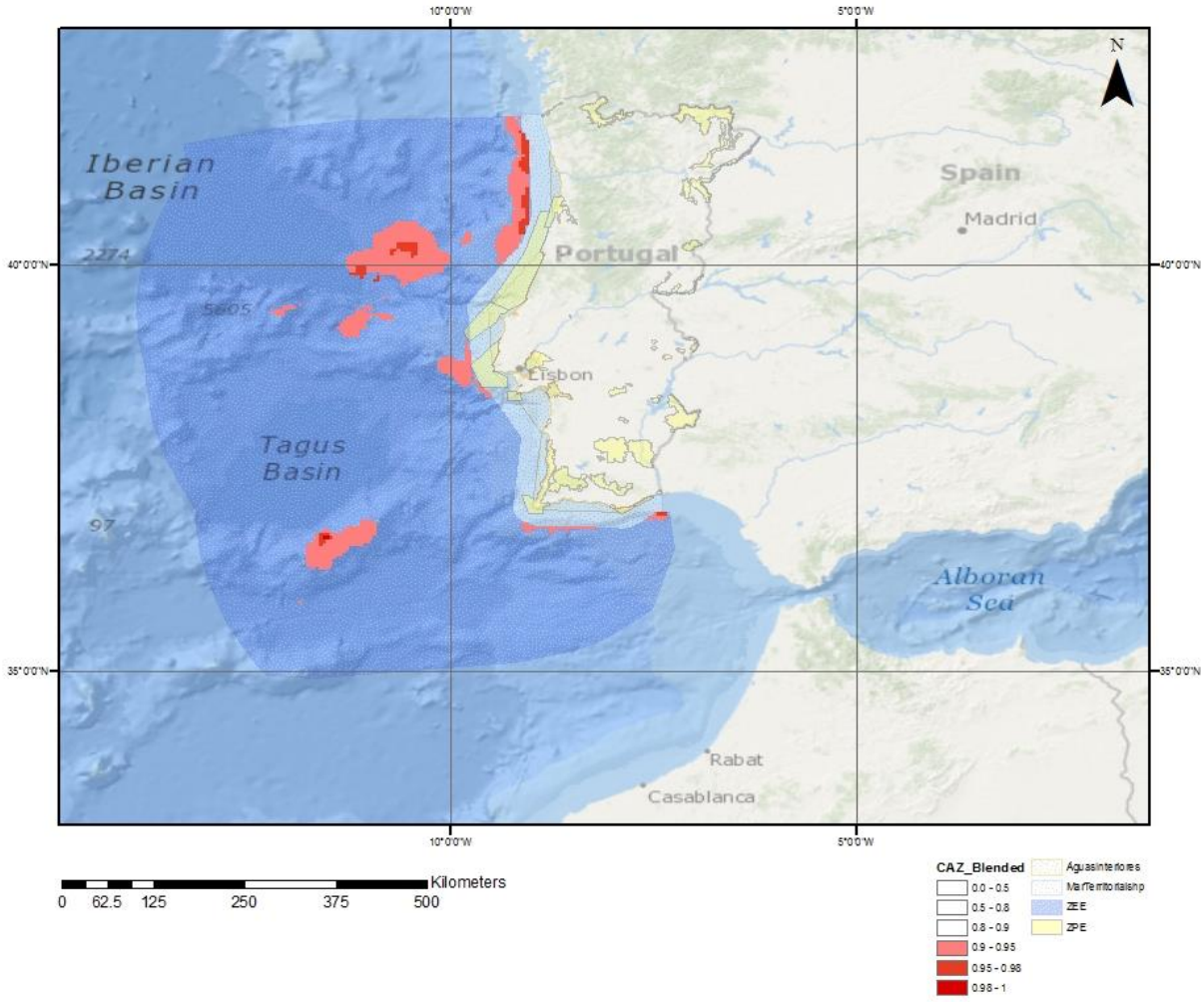

Figure 9 - High priority offshore areas for seabirds across mainland Portugal. Spatial prioritization results obtained by averaging the seasonal offshore priority areas for seabirds. High priority levels shown include the 10% and 2% Top Fractions.

Discussion

Spatial planning in the marine environment is a relatively recent management activity, when compared with land use planning (Peel & Lloyd 2004; Douvere & Ehler 2009). The overexploitation and the increase of human pressure on marine environment has amplified the need to identify and conserve important ecosystems at sea (Smith et al. 2014). Implementation of efficient MPAS, management plans and conservation actions for seabirds demands robust information on species distribution during each phenological stage of its life cycle. Furthermore, important seabird areas constitute valuable information toward marine conservation efforts, as they can be indicative of productivity hotspots for a diversity of life, including primary producers, invertebrates, fish, and/or marine mammals (Piatt et al. 2007; Suryan et al. 2012). Marine IBAs can therefore provide a starting point for establishing legal protections, such as MPAs or SPAs, because they are designed using observational data and a standardized global criteria (Nur et al. 2011; Ronconi & Clair 2012; Lascelles et al. 2012). In addition, IBA data can have both regional and global applications, such as environmental assessment, design of best management practices, or broad-scale integrative marine spatial planning.

Analytical issues

Our approach clearly reflects the utility of a spatial planning tool like Zonation. The selected workflow allowed to integrate a considerable amount of information on seabird distributions, at broad spatial and temporal scales, to provide a simple, balanced and objective identification of the most relevant areas for conservation. The final framework is a well-justified proposal for expansion of the existing SPAs network, as well as a valuable contribution for future implementation of MPAs in Portugal.

Three major aspects stand out from Figure 9. First, the importance of continental shelf areas, especially along Nazaré-Minho area and off Cape Raso Coast. Seabirds usually show

a numerical response in relation to food availability (Schreiber & Burger 2002) . Shelf edge areas, north of Nazaré are highly productive offshore areas, due to upwelling systems and oceanographical fronts that can support large numbers of seabirds. The attraction of seabirds to these edge areas may also be related with fisheries effort and fishery discards. Trawlers persistently operate along the shelf, attracting large numbers of offal-eating seabirds. So, migratory and breeding seabirds in this region, benefit from human fisheries in the area, by foraging on food items that would otherwise be unavailable to them.

Second, the importance of a group of 3 offshore areas encompassing: the abyssal plain between Porto Seamount and S. Pedro canyon; the area north of Carvalho Araújo Trough; the area Estremadura Spur and Duarte Pacheco Spur. These 3 areas present high diversity of geological formations, like canyons, seamounts and abyssal plains. Though, the most relevant aspect is that these 3 areas are all associated with smoother slopes zones and more moderate continental shelf rise than other continental shelf areas. During Autumn and Winter, this group of 3 areas is influenced by WIWiFs, Western Iberia Winter Fronts.

The third area shown in this Figure is the Gorringe Ridge-Ampère Seamount area. This is a well known region characterized for its high productivity, due to the influence of the ACEB, Azores Current Eastern Branch, and biodiversity (ICNF 2015).

Implications for marine conservation planning in Portuguese continental waters

Understanding the patterns of seabird distribution is crucial to the definition of MPAs (Amorim et al. 2009), but the identification of truly oceanic important areas for seabirds is still a challenge (Arcos et al. 2012). Most often the spatial planning for seabird conservation focus on protection of breeding areas with much less attention given to feeding, resting, migratory and wintering areas (Amorim et al. 2009). In this work, we followed a workflow that allowed to identify relevant areas for conservation of marine bird diversity on Portuguese offshore waters (Lehtomäki et al. 2009; Lehtomäki & Moilanen 2013), not relevant as breeding areas, but important as feeding, resting, migratory and wintering

grounds for migratory and highly mobile species. The output areas can be considered as an ecologically well-justified proposal for future implementation of MPAs and expansion of the current marine Natura 2000 network outside the Portuguese territorial waters.

Our results address many of the planning needs Portugal has for the marine environment. Recent SPA designation focused on designation of protected areas on territorial waters excluded offshore areas. This work shows that there is a necessity for designating protection areas in non-coastal zones, which are also ecologically important for seabirds during their annual life cycle. Some of the identified key areas are in regions thought to be important for marine biodiversity, due to their environmental characteristics (e.g. Gorringe Bank). Indeed, the majority of IBAs are associated with physical features that influence productivity and/or cause upwelling and mixing (Smith et al. 2014; Lascelles et al. 2016). Other proposed areas are located on the border of the EEZ and the territorial waters' limit. Some of the proposed areas can be consider an extension of current nearshore SPAs.

These results are also very relevant to undertake in the future best practice management actions, aimed at identifying potential conflict areas with anthropogenic activities and minimize their impacts. In general, fisheries are considered to be the major conflictive activity with marine biodiversity conservation (Croxall et al. 2012). But on offshore areas there are several other pressures that might affect species ecological niches (Lascelles et al. 2016). For instance, recent prospection for oil and gas in offshore areas of the Portuguese EEZ can lead to the development of drilling infrastructures in the near future. Seabirds are also very sensitive to marine traffic and pollution (Croxall et al. 2012; Winiarski et al. 2014; Lascelles et al. 2016) which is likely to increase. Therefore, there is a crucial need to understand the environmental factors driving the distribution of marine birds and other species in the region and implement a robust SCP approach, based on well set conservation objectives. Specific conservation actions should also be integrated in a larger national management plan in order to consider the flux of individuals and populations between distinct MPAs.

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Chapter 5

General Discussion

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This thesis investigates the movements and distribution of pelagic and neritic seabirds and uses modelling approaches to identify the environmental factors that affect their spatial occurrence. From this work, it is clear that overall productivity parameters (SST and Chlo-a) are good predictors of species presence (Chapter 2 and 3), most likely due to their link with availability of resources, whilst species ecology and seasonality making other variables contributing differently for a given species at a given time (e.g. “distance to colony” in the breeding season). Although inter-specific variation is expected and should be considered when designing conservation measurements, intra-specific variation is also quite relevant particularly between the sexes, which might have distinct requirements (Chapter 3). Predictive models are only as good in their ability to produce valuable outcomes as the data that is inputted into them. It is therefore paramount to collect good quality empirical data and to process environmental data with the highest definition possible (also considering the tracking resolution) and most importantly to select an adequate modelling approach to the datasets (Chapter 4). Final decision making process in which to select which areas should be designated for protection status can be supported with prioritization techniques (Chapter4), and the methods show here can be of great for the conservation of marine systems.

Monitoring seabird spatial distributions

Understanding seabird spatial ecology, habitat preferences and movement patterns in pelagic areas is a task usually hampered by logistic and financial constraints (Ramírez et al. 2008). The most common study methods are ship-based or aerial censuses or individual

remote tracking, using data-loggers. There is a wide array of devices useful for seabird tracking (e.g. platform terminal transmitters (PTT) or acoustic telemetry tags), that can be combined with other technologies (e.g. accelerometers, depthmeters or temperature sensors) to better understand individual behaviour or measure environmental parameters of the selected habitats (Wilson et al. 2007; BirdLife International 2009).Positioning technology, precision, total device weight, attachment method, waterproofness, battery capacity, availability of solar panel recharge or remote data transmission (and type of technology used to do so) are some of the aspects that have to be taken into account when defining study species, experimental design, spatiotemporal resolutions and ecological questions to be addressed in seabird tracking studies (Wilson & Vandenabeele 2012; Hunt & Wilson 2012).

The results obtained in Chapter 2, based on remote tracking data of individuals of both species of Giant Petrels, using Geolocators (GLS), highlights the usefulness of this technology for predictive distribution studies, projected to macro (1000-3000Km^2) or mega-scales (>3000 Km^2) (BirdLife International 2009) and aimed to cover species annual life cycles. The major drawbacks of this technology are its low precision (100-200 km, (Phillips et al. 2004)) , since it is based on light readings that can be sometimes erroneous due to external effects and/or animal behaviour; and the fact that the bird has to be caught a second time for tag removal as this are loggers and require data downloading. Given the fact that it only allows to calculate two positions per day, and its low energy consumption rates, GLS are more suited for long term tracking, for instances to study migration ecology or seasonal differences in habitat use (Chapter 2).

Technological advances made Global Positioning System (GPS) devices widely available and more affordable for wildlife studies. Combined with other technologies like GSM/GPRS and supplied with solar charging capacity, it is now possible to use GPS on medium or long-term tracking studies, benefitting from its high spatiotemporal resolution capabilities and precision, and also allowing to remotely retrieve data in an automated process. The GPS/GSM system used on Chapter 3 of this thesis to track individuals of Audouin's Gull during the breeding season required the adaptation of several commercial technologies to develop an entirely novel solution for long-term seabird tracking. These new transmitters

were successfully used for the first time on a seabird and it enabled the longest tracking of this species so far anywhere in the world. This achievement allowed acquiring totally novel information regarding the species distribution during the entire breeding period. The new transmitters applied to seabirds (and developed in collaboration with members of CEABN/CIBIO) open new avenues of research for this group of species given the relatively low cost of these tags in relation to similar options currently commercially available.

Advantages of long-term monitoring schemes and multi-taxa approaches for Spatial Conservation Planning (SCP)

The integrative approach of incorporating multi-year data of species occurrence, available from long-term monitoring schemes, on predictive modelling and spatial prioritization procedures, using a temporal scale that splits the annual cycle in several seasons (Chapter 4), is a solution to incorporate stochastic inter-annual variations between homologous seasons in the Spatial Conservation Planning process, thus reflecting the dynamic nature of the marine environment. At the same time, this approach also allows to better understand intra-annual differences in space use by seabirds.

Optimal design of a protected area intended to conserve a given population would need to encompass that population's entire year-round distribution. While it may be possible to accomplish such a design for some resident or non-migratory species (Reeves 2000), the ranges of most seabird populations are often be too large for this to be practicable. Also, effectiveness of marine protected areas depends on their ability to protect different life stages and distributional ranges (nesting, feeding, and migrating grounds), as vulnerability of a population may be habitat and stage specific (Hooker & Gerber 2004; Yorio 2009). The inclusion, as much as possible, in the SCP process (Chapter 4) of distribution data for common and occasional, migratory and resident, threatened and least concern species, although with different relative weights in the spatial prioritization analysis performed, reflects the aim of minimizing the risk of not identifying important areas for seabirds in the final results.

The long-term and multi-taxa approaches allowed to obtain a more comprehensive picture of ecosystem's reality in the Chapter 4 results.

Spatiotemporal flexibility of marine protected areas networks

Marine protected areas (MPAs) have been proposed and used as a tool for seabird conservation worldwide (Duffy 1994 Hyrenbach et al. 2000; Yorio 2000, 2009; Wienecke & Robertson 2002; Airame et al. 2003; Garthe & Skov 2006; Lombard et al. 2007). To date there have been relatively few Natura 2000 sites identified for the offshore marine environment and this represents the most significant gap in the Natura 2000 network (European Commission 2007). Therefore, Chapter 4 of this thesis presents itself as case study in the European context and contribution to address this problem.

Scientific studies and technical guidelines suggest that boundaries of MPAs in open sea should be flexible enough to adapt to the range shifts of nutrients (Hooker & Gerber 2004; European Commission 2007; Claudet 2011; Ruiz-Frau et al. 2015), organisms and water masses, especially when MPAs focal species of concern are as highly mobile as seabirds, whose spatial distribution is more affected by prey densities and oceanographic variables than static physical features, as bathymetry (unlike the cetaceans) (Hooker & Gerber 2004).

A more adaptable proposal of MPAs boundaries definition accordingly with time of the year/phenology, using seasonal outputs from Spatial Conservation Planning processes (as presented in Figure 9, Chapter 4) could contribute to minimize the problem of MPAs inefficiency to effectively protect highly mobile seabird species.

Even if some doubt still subsists on the efficiency of offshore MPAs, at least they may pose a legal and regulatory framework to human activities, fact that is directly relevant for seabird conservation (Lascelles et al. 2012; Perrow et al. 2015).

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